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Movements of Drift Cards in Georgian Bay in 1953[1]

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ABSTRACT

Recoveries of drift cards indicate a generally easterly drift of surface water across Georgian Bay, corresponding to prevailing winds. No cards were recovered on the western side of the bay, suggesting persistent upwelling there.

PROCEDURE AND RESULTS

Georgian Bay is a major arm on the northeast corner of Lake Huron, to which it is connected by a relatively narrow and shallow opening, so that it is almost a discrete body of water. It is roughly a rectangle 50 by 100 miles with its long axis lying NW-SE. It is situated between latitude 44°30′ to 46° N and longitude 80° to 82° W.

Three drops of drift cards of the type described by Olson (1951) were made from the air in 1953, one in each of the months of June, July and August. The drops were confined to these months because much of the shoreline of Georgian Bay is uninhabited except during the summer holiday season. The cards were standard 4- by 6-inch postcards, sealed in short lengths of polyethylene tubing of material 0.002 inch thick. The cover was only moderately satisfactory, possibly because the material was so thin, in particular pinholes appeared to develop readily when the envelopes were abraded by the sand through wave action on beaches. However, in spite of such loss, 10% of the cards released were recovered. To facilitate dropping, the cards were bundled loosely in lots of fifty in brown paper fastened by tape that had a water-soluble glue. The bundles were dropped approximately 10 miles apart along two lines representing essentially the major and the minor axis of the bay, with three or four extra drops in the northwestern section off Manitoulin Island. The first package to be dropped was the most southerly one, the aircraft then proceeded northwest to the end of the major axis, southwest along the coast of Manitoulin Island and then, after veering south to take up its position, east along the minor axis. The packages were arranged serially with cards 1 to 50 being in the first drop. Cards 1 to 1000 were dropped in June, 1001 to 2000 in July and 2001 to 3000 in August. The cards were dropped from an aircraft of the Provincial Air Service based in Toronto. In the August run, bad weather forced the aircraft off its predetermined course, and the drops along the minor axis had to be made north of the intended positions.

The movements of the cards are shown in the three figures, one of which has been prepared for each drop. The figures show the points at which the bundles

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of fifty were dropped as circles. The arrows indicate where the cards were found and the number within the circle gives the number of cards returned from the drop in question. The date adjacent to each circle is the date of the first card picked up. Since the cards from a given drop scattered very little, it is presumed that all went ashore at nearly the same time and that the time of discovery of later arrivals, particularly in the remoter sections, was more a matter of the time the discoverer visited the vicinity than of the card being delayed in coming ashore.

Almost all the cards returned were found on the eastern half of the shoreline. It is particularly striking that none was found on the western shore of the southern half of the bay. This section of the shoreline is well inhabited, and if cards had landed there in any substantial numbers, some would have been surely picked up. The middle section of the northern coast is the least frequented and lack of returns from here cannot be regarded as of any significance except as it may confirm a general trend.

The two side panels in each figure illustrate wind records taken at two lighthouses in Georgian Bay, those on Lonely and Hope Islands. The wind records have been represented as wind tracks. These tracks are the path a body such as a piece of thistledown would be expected to follow if the wind strength and direction from day to day were as reported at the station concerned. This path is of course entirely fictitious as far as affairs in the air are concerned, for the thistledown and the air mass in which it was suspended would be far from the station in a day or so, and would in all probability then be moving in quite a different

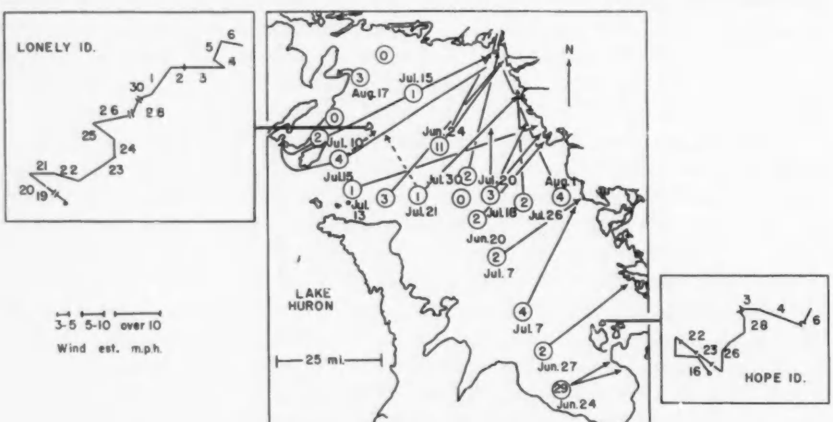

FIG. 1.—Returns from the June 16 drop. The circles indicate the drop points, the figures in them indicate the number of cards recovered from a drop of fifty. The arrows indicate where the cards were found and the dates are the dates of the first recoveries.

For explanation of the wind tracks in the side panels see text, above. The numbers associated with the wind tracks are the calendar dates, those dates left out of the series are omitted to keep the diagram clear. Crossbars indicate calm periods.

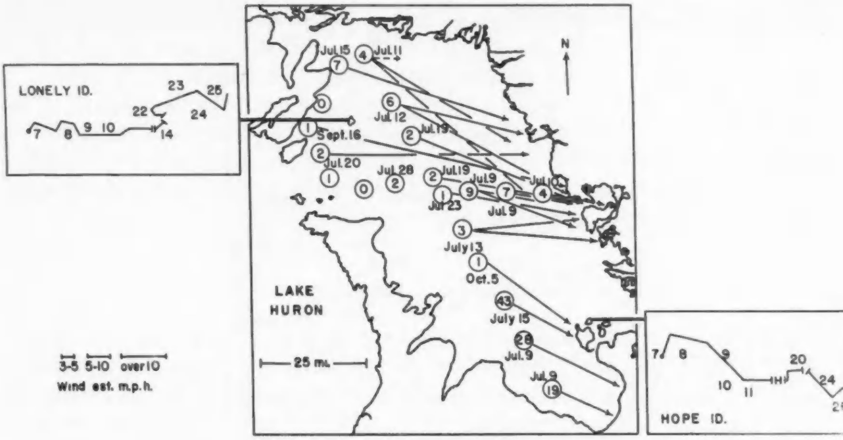

FIG. 2.—Returns from the July 7 drop.

direction from the new air mass then being observed at the station in question. However the wind track as shown is not so much at variance with the movement of a particle suspended in the surface water on which the wind acts, for in this case the movement of the water is much slower than that of the air and a particle in the water will be subject to the effects of air movement at the observation station on successive days for some time. The scale on which the wind tracks are plotted is only semi-quantitative for there is not a continuous wind record at the lighthouses. The length of the track for a given day is based on the lightkeeper's estimate of the general wind direction and strength for the day. It is unfortunate that no wind observations were available for the northeastern and mid-eastern sections of the bay, for no doubt there are local differences in the winds there, as there are between Lonely and Hope Islands.

The movements of the cards, and with them presumably the surface waters, appear to be strongly under the influence of the winds, as Verber (1953) showed with similar material in Lake Erie. This can be seen by comparing the wind tracks with the card movements in the three figures.

The June drops were noteworthy for their tardiness in coming ashore. This may be partly due to lack of prompt discovery, since the holiday season which brings cottagers to the shore is not under way until July; but in many cases the first June returns were not received until after the corresponding July cards had come ashore. This slow arrival is in accordance with the wind records. During the week after the drop, the winds were in general southeast and would be expected to take the cards farther away from the shore on which they ultimately landed. After a brief northwest interval in which the winds might have possibly returned the cards essentially to the positions where they had been dropped, the winds set in steadily southwest until the time of the next drop. The westerly winds after July 7 then, presumably, brought the cards ashore well north of where

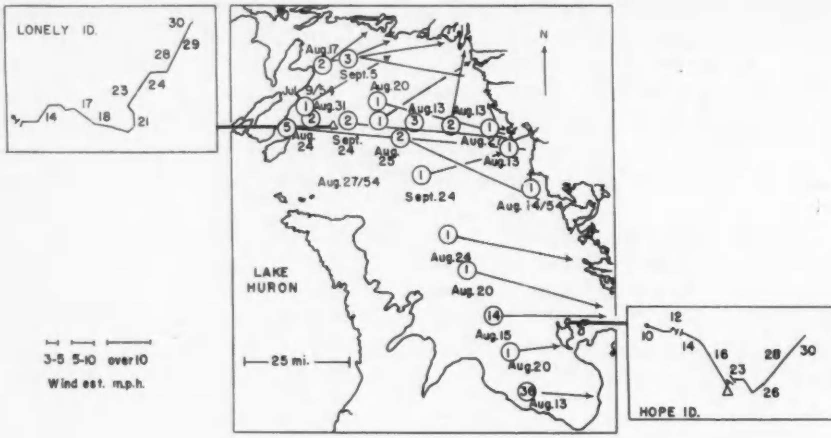

FIG. 3.—Returns from the August 10 drop.

they had been released. On June 20 three cards from the third-to-last drop along the minor axis were picked up by a gillnet fisherman about 20 miles due north of the drop point. Several other cards were observed in the vicinity but were not retrieved. Six cards from this drop were subsequently found on the shore west of the point where the three were picked up on June 20 the first of these being found on July 18.

Cards dropped along the minor axis appear to have gone too directly north to have been carried by a surface movement of the water directly down wind. The movements of these cards suggest an area of convergence of the surface currents in the northeast corner of the bay, associated with downwelling there. Three cards of the June drop were still floating well off shore on September 22. These were from the western end of the minor axis and are indicated by the dotted arrows. Two cards of the June drop both released near the connection of Georgian Bay to lake Huron escaped from the bay. These were the only returns from outside Georgian Bay in the whole series.

In July there were steadier winds following the drop, and many cards were ashore within two or three days of being released. Again convergence of certain of the recoveries, this time a more southerly tendency of the northern drops, suggests downwelling along the eastern shore. One card of the July drop was still floating September 17 as indicated by the dotted arrow at the north end of the major axis.

The August results again follow the wind pattern. They were slightly slower in coming ashore in conformity with the slightly lesser wind strengths reported. Convergence is again suggested in the northeast corner, with cards again travelling north up the eastern shore from four of the last five drops along the minor axis.

The westerly section of the bay appears to be a region of persistent upwelling since no cards were ever found stranded along this shore.

While the drift cards dropped in Georgian Bay respond to the wind pattern, the area appears to be large enough to damp out the day to day variation, and to reflect the statistical pattern of the prevailing winds. The water movement suggested by the cards in 1953 conforms well with the mean surface water temperature pattern described by Millar (1952) for the period 1935–1941.

In particular there is no evidence of a major escape of surface water from Georgian Bay into Lake Huron.

ACKNOWLEDGMENTS

The investigation was carried out with the support of the Ontario Fisheries Research Laboratory, Department of Zoology of the University of Toronto, the Research Council of Ontario and the Research Division of the Ontario Department of Lands and Forests. Mrs. J. C. Budd superintended the packaging of the drift cards and released them. The Parry Sound office of the Department of Transport Marine Services kindly supplied transcripts of the lighthouse diaries from which the wind data were taken.

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Basic Productivity of Trevor Channel and Alberni Inlet from Chemical Measurements[1,2]

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ABSTRACT

Chemical properties of the waters in Trevor Channel and Alberni Inlet during late summer have been applied for an estimate of basic productivity. Based on the assumptions that the deep water in the system is renewed once per year and that the observed conditions in September represent the state of the water just before renewal, the oxygen deficit and the phosphate surplus in the deep water have been used as a measure of the organisms decomposed during the year. Oxygen depletion gives 28 g/m^2 of plankton per year as carbon; phosphate liberation gives 31 g/m^2. From fishery statistics it was estimated that the herring in Barkley Sound consume about one-quarter of the available plankton and all plankton feeders consume about one-half of the total. This would increase the above figures of productivity to 56 g/m^2 and 62 g/m^2, respectively. These values are probably a minimum annual productivity inasmuch as basic assumptions may not be completely fulfilled. Regeneration of nutrients in the surface layer, and some renewal of deep water by mixing and circulation, probably occur throughout the year.

INTRODUCTION

Early work on British Columbia inlets (Carter, 1933) showed them to be unproductive with few exceptions. Where the inlet is a typical fiord with a stream of cold, silty glacial water at its head, the plankton populations are small except at the mouth. This condition is general because of the poor light penetration in the turbid water, the small nutrient content of the tributary streams, and the low temperature of the glacial water. Hutchinson and Lucas (1931) showed the area of the largest standing crop of phytoplankton in the Strait of Georgia to be in the region of greatest mixing between the sea water and Fraser River water at the island boundaries of the strait. The smallest populations were in the immediate vicinity of the Fraser River and those of average size were in the areas dominated by sea water. In his study of plankton distribution in British Columbia inlets, Le Brasseur (1954) found the same relative distribution with very low concentrations at the head of the inlets increasing to a maximum at the mouth and then decreasing again outside the inlet. Dissolved oxygen concentrations observed near the surface at the mouths of inlets (Pickard, 1954) are extremely high with values in excess of 150% saturation in some cases.

Tully (1949) conducted the classical research on Alberni Inlet. He made a thorough study of the physical phenomena in the inlet and postulated a mechanism of water movements which has been accepted generally as typical of a deep

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inlet (Ketchum, 1951; Stommel and Farmer, 1952). His basic hypothesis for water exchange will be applied here in the study of chemical characteristics.

Alberni Inlet is a typical British Columbia fiord (Fig. 1). It is 21 nautical

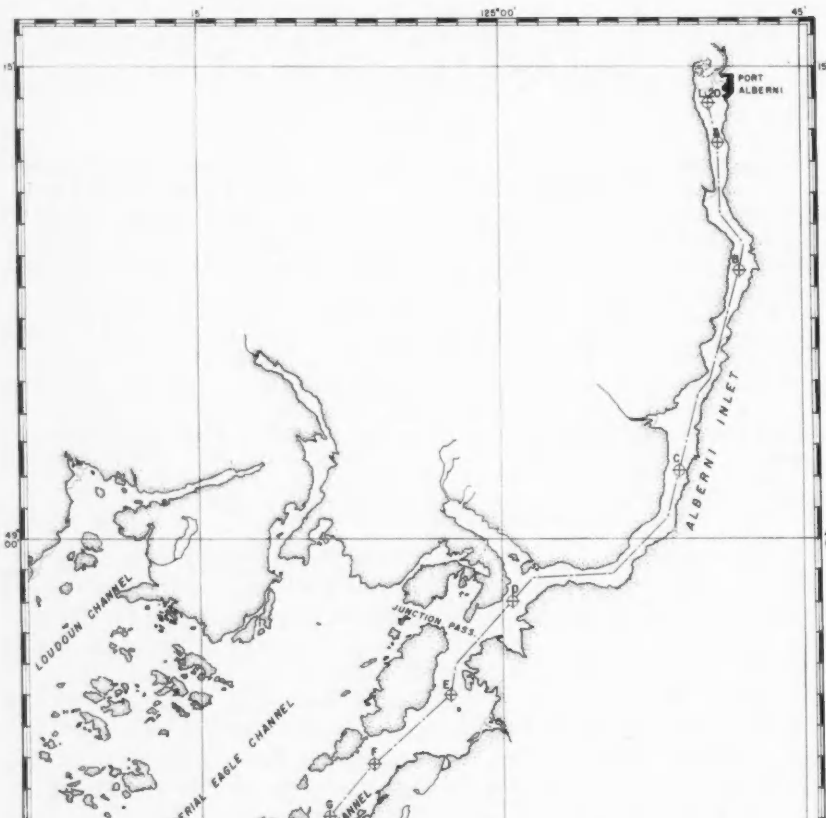

FIG. 1.—Chart of Barkley Sound and Alberni Inlet showing line of stations.

miles (39 km.) long, 0.6 naut. mi. (1.1 km.) in average width and up to 200 fath. (360 m.) deep. Rocky, precipitous shores rise in excess of 1000 ft. (300 m.) and a valley with the Somass River estuary is at the head. Extending into Trevor Channel its bottom topography is characterized by three sills which divide the inlet system into three basins along its length. The inlet differs from Norwegian fiords in that its outer sill through Trevor Channel is quite deep at 20 fath. (36 m.) and permits a regular exchange of intermediate water. An even deeper side entrance through Junction Passage allows circulation with the Pacific Ocean to a depth of 46 fath. (85 m.). Winds conform to the orographic effect of the mountains and are either northerly or southerly. Strongest winds blow up the inlet from the south during summer. Precipitation is relatively high at an average of 67 inches (170 cm.) per year (Meteorological Division, Climatic Summaries, 1948). Winter is the season of largest runoff. Comparatively little precipitation occurs from March to October with a dry spell usually prevailing during late summer. Snow persists only occasionally during cold winters.

Trevor Channel as well as other parts of Barkley Sound are noted for their valuable herring fishery. Alberni Inlet and its tributary rivers carry substantial runs of sockeye, spring and chum salmon which support a small commercial fishery. Coho and spring salmon as well as steelhead trout provide a popular sport fishery in the inlet and rivers.

The present work is an attempt to evaluate the productivity of an inlet system, Trevor Channel–Alberni Inlet, from chemical measurements on the environment. Such an evaluation can be only an approximation at its best. It does not necessarily imply that the calculated production was actually achieved, but only that the system has the capacity or potential for that production. In such a study the complexity or physical, chemical and biological factors must be at least recognized. Corroborative evidence for any conclusions must be drawn from various approaches.

SURVEY DATA

The survey was conducted during the week of September 7 to 11, 1954. Weather conditions improved from a heavy rain with strong southeast winds (25 m.p.h.) on the morning of September 8 when the survey commenced, to calm, sunny and warm weather on September 9 and 10.

Samples for salinity, dissolved oxygen, pH and phosphate were taken at surface, 6, 15, 30, 45, 60, 90, 150, and 300 ft. (0, 1.8, 4.5, 9.1, 13.6, 18.2, 27.2, 45.4, and 91 m.) and near bottom, or at as many of these levels as the depth permitted. Sampling bottles of the Fjarlie (1953) design were used for subsurface samples. Surface water was collected with a bucket. Salinity samples were sealed with wax and analysed at the base laboratory of the Pacific Oceanographic Group after the survey. Dissolved oxygen, pH and phosphate determinations were carried out on board ship within 24 hours after the samples were taken. Phosphate analyses were repeated in the base laboratory 10 days after the survey.

The procedure described by Tully (1949) for shipboard dissolved oxygen analysis was used. A Beckman pH meter (a–c., 110 volts, model H2) was employed for the pH determinations. It was standardized with a buffer solution of Coleman pH buffer tablets dissolved in distilled water. Inorganic phosphate analyses were conducted by the method described by Robinson and Thompson (1948). A Klett-Summerson colorimeter with No. 66 filter and 4.5-cm. cell was used to measure the colour intensity. Owing to unsteadiness of the instrument in rough waters, measurements were made while the ship was tied up or standing on station.

OBSERVED DISTRIBUTIONS OF PROPERTIES

The data from station H in Trevor Channel to L 20 in Alberni Harbour have been plotted in sections shown in Figures 2 and 3. Figure 2 shows the distribution of conservative properties (variables unaffected by biological processes),–salinity, temperature and density. The stratification in salinity is shown very clearly with fresh water confined to the upper 3 m. for most of the inlet. The deep water below 60 m. exceeds 32‰ in salinity. This is the water which has flowed in from the continental shelf area on the west coast of Vancouver Island. A temperature distribution very similar to that of salinity is shown in Figure 2b. The density stratification and the large stability of the water column owing to the fresh water inflow have permitted considerable surface warming in the upper inlet. Less density stratification and more wind mixing in Trevor Channel have reduced the vertical temperature gradient. The density picture, as depicted by the σ_t distribution in Figure 2c, is largely governed by the salinity distribution. During the summer months of surface heating, temperature distribution also corresponds to the density pattern.

Figure 3 shows the distribution of non-conservative properties, that is, those properties which are affected by biological processes. In Figure 3a is shown the dissolved oxygen distribution. The lowest dissolved oxygen content is in the deep water of Trevor Channel outside the entrance to Alberni Inlet where concentrations of less than 2 mg/l (milligrams per litre)[3] are found. This water has undergone oxygen depletion by natural oxidation processes occurring in the deeps off the continental shelf and at the bottom of the inlet. Absence of similar oxygen minima near the bottom in the upper part of Alberni Inlet suggests less planktonic material settling in that region. The highest oxygen concentrations occurred at the entrance to Alberni Inlet (stations D and E) at depths down to 10 m. This high oxygen content is due to photosynthesis by concentrations of phytoplankton in the upper sunlit layer. At station H on the threshold to Trevor Channel, deep mixing by winds and tidal currents causes a relatively homogeneous distribution of oxygen.

The phosphate distribution shown in Figure 3b is a further independent check on the water movements and biological processes. The highest phosphate

[3]To convert to milligram-atoms per litre, the more common unit for dissolved oxygen in oceanography, divide by 16.

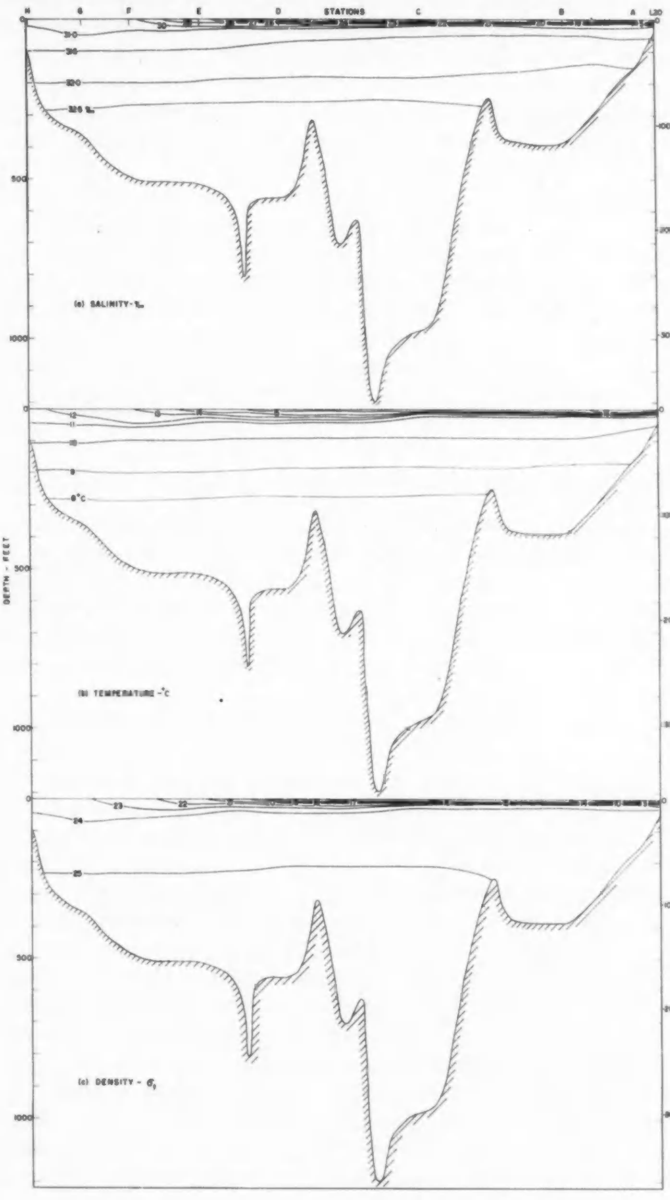

FIG. 2.—Vertical distribution of conservative properties in Trevor Channel–Alberni Inlet.

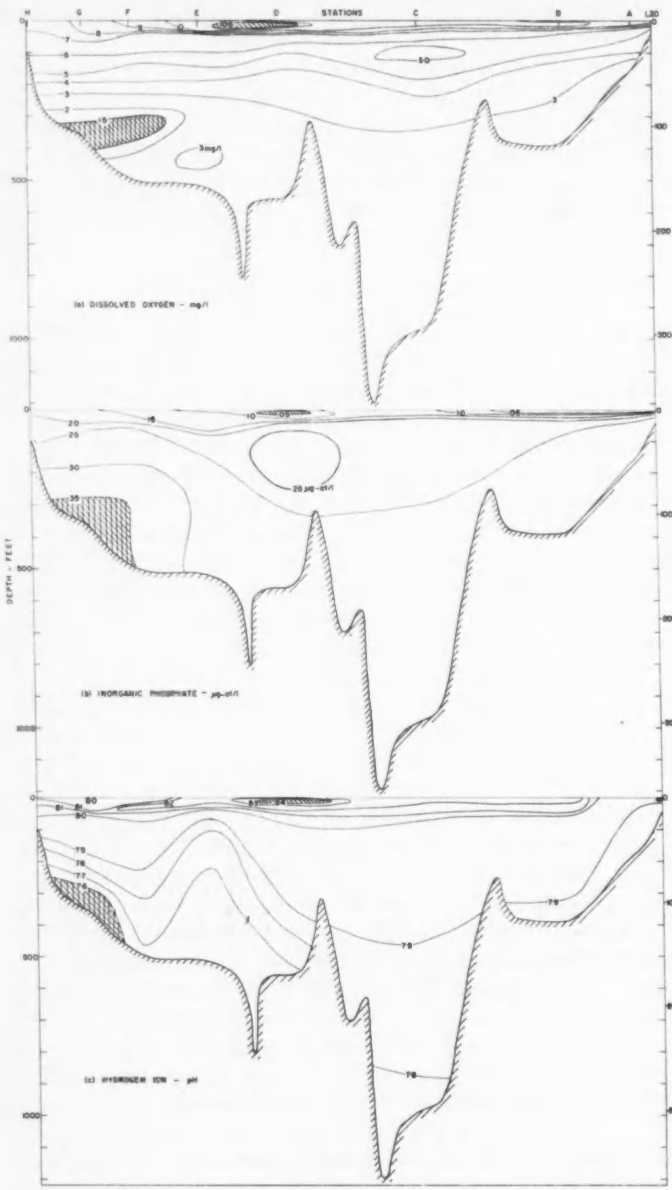

FIG. 3.—Vertical distribution of non-conservative properties in Trevor Channel—Alberni Inlet.

concentration was found in the zone of low oxygen. These factors are parallel in showing that a state of organic decomposition is taking place with a very slow changeover of water. Phosphate-poor water occurs in the surface layer at stations D and E, a result of phosphate removal by plankton. Low phosphate concentrations also characterize the surface waters at the head of the inlet. This condition results from the inflowing Somass River water observed to be practically devoid of phosphate.

The pH distribution shown in Figure 3c conforms quite closely to both the oxygen and phosphate pictures. Deep water of low oxygen content just inside the threshold sill exhibits a low pH, the result of increased carbon dioxide caused by oxidative processes. High pH near the surface is associated with high oxygen content and a large phytoplankton population. Here the carbon dioxide–bicarbonate–carbonate equilibrium has been shifted toward a smaller carbon dioxide concentration. At the upper end of the inlet a low pH is the result of decomposition of pulp mill wastes, which is also reflected in a reduced dissolved oxygen concentration.

APPLICATION OF CHEMICAL OBSERVATIONS TO BASIC PRODUCTIVITY

Seasonal changes which occur in the concentrations of dissolved gases and nutrient constituents can be correlated with the processes of photosynthesis and respiration provided the effects of water movements and mixing are understood. Although a complete seasonal picture of the required variables is not available at present, enough data from other sources can be examined to provide a basis for estimates of productivity.

Oxygen Depletion, Phosphate Liberation and pH Reduction in the Deep Water

The deep water just within the threshold sill in Trevor Channel displays very low oxygen, high phosphate and high hydrogen-ion concentrations. This condition is not characteristic of the water flowing into the system, which has been studied on a seasonal basis (Tully, 1949). Inflowing intermediate water generally has the characteristics exhibited just above sill depth shown by the distribution of properties at 85 m. between stations D and E. The state of the deep water can only be a result of local processes of decomposition with the removal of oxygen, release of carbon dioxide and liberation of phosphate. If it is assumed that the deep water in the basins of Trevor Channel and Alberni Inlet is replaced at least once a year as suggested by Tully (1949, p. 73), then the oxygen, phosphate and hydrogen-ion concentrations are altered locally by biological processes during the intervening period. The decrease in dissolved oxygen below 85 m. can be attributed mainly to the decomposition of organisms.

It is assumed that the original water reaching the depth below 85 m. was at the same oxygen concentration as that observed just above 85 m. The dissolved oxygen concentration of the water entering the deep basin of the inlet is 3.0 mg/l while that of the deep water is 1.5 mg/l (Fig. 3a). A difference in concentration

of 1.5 mg/l is obtained, which is equivalent approximately to the oxidation of $41/109 \times 1.5 = 0.563$ mg/l of carbon or $0.563/0.44 = 1.28$ mg/l of dry plankton (Sverdrup *et al.*, 1946, p. 237).

Similarly, the increase in phosphate from intermediate depth to 100 m. can be used as a measure of organic decomposition and ultimately productivity. The concentrations found at the two depths were 3.0 and 3.5 μg-at/l (microgram-atoms per litre) or an increase of 0.5 μg-at/l. This corresponds to a phosphorus increase of 15.5 μg/l or the decomposition of $15.5/0.011 \times 10^{-3} = 1.41$ mg/l of dry plankton (Sverdrup *et al.*, 1946, p. 929) in reasonable agreement with the oxygen data. If the thickness of this zone of low oxygen and high phosphate concentrations is considered to be 50 m., the basic productivity would amount to 64.0 g. of dry plankton per square metre of surface area for the oxygen data and 70.5 g/m^2 for the phosphate data.

Hydrogen-ion concentration from pH data can be used for determining productivity but only in conjunction with measurements of carbonate or bicarbonate alkalinity. From this can be evaluated the carbon dioxide increase and hence the amount of organic material decomposed. Unfortunately, in the present data there are no alkalinity determinations. It is noteworthy, however, that a pH change of 0.5 from surface to bottom was incurred by the carbon dioxide added from organic decomposition.

Oxygen Supersaturation in the Euphotic Zone

Accumulation of oxygen in the zone of photosynthesis gives a measure of phytoplankton outbursts. Only minimal values are obtained because some oxygen is given off to the atmosphere in mixing. Respiration by zooplankton and bacteria further suppresses the oxygen peak. The surface water of Trevor Channel contained up to 10.5 mg/l of dissolved oxygen at 3 to 5 m. depth. At the prevailing salinity and temperature this corresponds to a value of 120% saturation. If the supersaturation is attributed entirely to phytoplankton activity, then the difference between 10.5 mg/l and 8.6 mg/l (concentration at 100% saturation) gives the dissolved oxygen contributed by photosynthesis. From the simplified chemical expression for photosynthesis,

$$6CO_2 + 6H_2O \xrightarrow{\text{energy}} C_6H_{12}O_6 + 6O_2$$

6 atoms of carbon are combined into an organic form with the release of 12 atoms of oxygen. For every gram of oxygen produced $72/192 = 0.375$ g. of carbon are assimilated. Thus for the 1.9 mg/l of dissolved oxygen above saturation value there are 0.712 mg/l of carbon used up. This amounts to $0.712/0.44 = 1.62$ mg/l of dry plankton. Inasmuch as this is only an autumnal bloom of phytoplankton and the vernal bloom is at least of the same intensity, a minimum annual productivity of 3.24 mg/l of dry plankton is obtained. For a depth of 10 m. of the oxygen supersaturation zone in Trevor Channel the weight of dry plankton synthesized would amount to 16.2 g/m^2. This is less than one-quarter of the value obtained from oxygen depletion and phosphate liberation in the deep water and

indicates that a better seasonal study is required for a productivity estimate from oxygen supersaturation.

Phosphate concentrations in the surface water are low. In addition to depletion by photosynthesis, there is also the dilution effect of runoff. Consequently, seasonal variation of phosphate in the surface layer cannot be used for quantitative evaluation of productivity.

DISCUSSION

An evaluation of productivity from chemical measurements in Trevor Channel and Alberni Inlet demands, first of all, a knowledge of the circulation as a working hypothesis. Recourse may be made to the mechanism of water exchange postulated by Tully (1949) as well as basic principles involved in inlet circulation (Pickard, 1953). The chemical factors dealt with here—dissolved oxygen, phosphate and pH—are non-conservative properties, that is, their concentration may be affected by advection (circulatory processes), diffusion (mixing) or biological activity. It is necessary to separate the biological from the advection and diffusion processes in an analysis for productivity. Temperature and salinity can be regarded as conservative properties at depths below the effect of surface dilution, evaporation and heating because they are unaffected by biological activity. These properties facilitate the study of the effect of circulation.

A continuous process of replacement occurs in the deep water of Alberni Inlet. The extent of this replacement fluctuates with the density of the inflowing water. Dense water will promote more rapid flushing than light water as shown in model studies of Puget Sound (Barnes *et al.*, 1954). With the intrusion of dense Pacific water during late summer, flushing is greatly accelerated. In a matter of a few autumn months the whole system may be flushed, whereas only minor changes occur during the remainder of the year.

Tully (1949, p. 73) suggests that the deep water is replaced at least once a year. A basic assumption made here is that this water is replaced *only* once per year. Moreover, it is assumed that the conditions observed represent those just prior to the autumnal turnover. Evidence from the seasonal changes in water properties observed by Tully and the topography of the inlet show that these assumptions are not too unrealistic. The trend in isohalines and isopycnals at the time of the survey (Fig. 2a and c) shows that the inward flow over the Junction Passage threshold does not follow the bottom contours but maintains an almost horizontal course at intermediate depth. This indicates that the deep water is of some age greater than the intermediate water.

The characteristics of Pacific water entering Juan de Fuca Strait can be regarded as essentially the same as those for the Alberni Inlet deep water entering through Junction Passage. They come under the influence of summer upwelling off the west coast of Vancouver Island (Tully, 1942; Pickard and McLeod, 1953). Surveys made in Juan de Fuca Strait in March, 1953, and September, 1952, (unpublished data) show intermediate water properties there to be comparable to Barkley Sound deep water. It is true that water of low oxygen and high phosphate content has been observed intruding into Juan de Fuca Strait during late summer

(Igelsrud *et al.*, 1936). But this water enters at depths greater than 100 m. since the entrance to Juan de Fuca Strait is unobstructed to a depth of 200 m. The seaward entrance to Trevor Channel, on the other hand, is only slightly deeper than 30 m. Greater depths than this are generally absent at the chain of islands separating Trevor Channel from the remainder of Barkley Sound, except at Junction Passage. This narrow channel is connected to the Pacific Ocean at 45 fath. (82 m.). Water entering Trevor Channel through Junction Passage can only have a maximum density representative of 85 m. depth on the continental shelf of the west coast of Vancouver Island. Table I shows a comparison of the water properties in Juan de Fuca Strait with those observed in Trevor Channel at 30 and 85 m. Juan de

TABLE I.—Characteristics of the water entering Juan de Fuca Strait and Trevor Channel at 30 and 85 m.

Property	Juan de Fuca Strait off Pillar Point (48° 18′ N; 124° 03′ W)				Trevor Channel off Junction Passage (48° 55′ N; 125° 03′ W)	
	September 1952		March 1953		September 1954	
	30 m.	85 m.	30 m.	85 m.	30 m.	85 m.
Salinity ‰	31.7	33.7	31.9	32.3	31.5	32.55
Temperature °C.	9.5	6.9	7.3	7.3	10.1	8.10
Density σ_t	24.5	26.4	24.9	25.3	24.2	25.35
Dissolved oxygen *mg/l*	6.9	3.1	7.2	6.0	6.3	3.0
Dissolved oxygen %	68	33	74	64	68	31.2
Phosphate *μg-at/l*	2.41[a]	2.50	...	...	2.40	2.89

[a]Data from Juan de Fuca Strait off New Dungeness (48° 16′ N; 123° 04′ W), September, 1953.

Fuca Strait water in September has a smaller oxygen saturation value than it has in March but does not approach the low value observed in the deep water of Trevor Channel. This precludes any likelihood that the low oxygen found at the lower end of Trevor Channel is a relict of the characteristics found in intruded water at certain times of the year.

Having established the required circulation pattern and the characteristics of the water entering the inlet system, we must set up certain basic assumptions for the subsequent treatment:

(1) Oxygen depletion and phosphate regeneration at depth are entirely due to decomposition of the dead planktonic organisms which have settled from the euphotic zone. Oxygen removed by the bottom muds is negligible.

(2) Area covered by the settling plankton is of the same magnitude as that occupied by the living population.

(3) Oxygen supersaturation near the surface is a result of photosynthesis.

(4) Net loss of plankton from the system owing to the seaward drift of surface water is small.

(5) The extent of regeneration of nutrients in the euphotic zone is unknown and neglected in this analysis.

(6) Amount of plankton removed by fish is small compared to that which settles. Otherwise the necessary correction should be applied.

The first three assumptions have been discussed already and need no further elaboration. With regard to (4), the seaward drift of plankton at the surface is compensated by a return flow at intermediate depth. As the plankton sink, their seaward drift decreases and may completely cease or reverse. In the final course of events the plankton propagated at stations D and E are near the bottom at F and G, a total drift seaward of some 6 miles.

Assumption (5) presents one of the major objections to the use of nutrient changes in the environment as a measure of productivity. It is argued that the nutrients in the upper layer of the sea can be reused several times in the course of a year. Thus, it is concluded, the nutrient depletion near the surface and addition in the deep water is not a true reflection of organic production. Although no quantitative measurements have been reported in the literature to show the extent of such regeneration, Riley (1951) recognized its probable existence. He chose a "round number" of 10% of the surface production as the deep-water oxygen consumption for the open ocean. Moreover, he showed that the minimum estimates of phosphate utilization, based on observed seasonal changes, range up to five times the calculated deep-water total. If nutrient regeneration in the euphotic zone inshore can be compared to that offshore, the estimates of productivity made here may be from five to ten times too small. Because the thickness of the euphotic zone is much smaller inshore than it is offshore, it can be assumed that regeneration of nutrients near the surface inshore is comparatively small. Nevertheless, this does not vitiate the fact that productivity figures given here may be grossly underestimated and are at their lower limit.

To establish the validity of (6) it is necessary to make some estimates of the plankton grazed by the fish. According to Hourston (personal communication), herring spawn and spend their early post-larval stages in Barkley Sound. The larvae appear to concentrate within the upper 10 metres during darkness where they apparently feed on the zooplankton. After they reach a weight of 7 to 8 grams in their first year they migrate elsewhere to feed. The adults return when they are an average of three years old weighing about 100 g. (Stevenson, 1950). From the population of adults in 1953–54 which was an average "good" year (Taylor and Outram, 1954) it was computed that there would be annually 700 million juvenile herring in Barkley Sound to produce such a crop of adults. Hourston (personal communication) suggested that field work showed 1954 to be a good year for juveniles. For an average weight increase of 7 g. per fish while the juveniles are in Barkley Sound, there is a total of 5 million kilograms (5×10^9 g.) added to the herring biomass. The water area of Barkley Sound is roughly 100 naut. mi.^{2} or 350 km^2. If the 5×10^9 g. of annual weight increment were spread evenly over Barkley Sound an average of 14.3 g/m^2 per year would be obtained. Allowing 0.17 g. of dry organic matter per gram of fish (Harvey, 1950), the 14.3 g/m^2 of fish would be equivalent to 2.43 g/m^2 of dry organic matter. According to Harvey (1950) there is a 30% loss in the food chain from phytoplankton to zooplankton and a 90% loss from zooplankton to herring due to respiration. The 2.43 g/m^2 of dry organic matter would have been derived ultimately from 34.7 g/m^2 of dry phytoplankton. If the herring comprise half of the plankton feeders in Barkley Sound, which also include anchovy, sand lance, young salmon and squid, the total

phytoplankton contributing to fish food likely does not exceed 70 g/m^2. Plankton consumed by bottom fauna such as clams, barnacles and other crustaceans may be equivalent to that assimilated by plant-eating organisms in the water column, according to Harvey (1950) from observations in the English Channel. But with these slow-growing bottom animals much of the food consumption goes toward their maintenance. Thus products of metabolism contribute toward oxygen consumption, carbon dioxide liberation, and nutrient regeneration just as in bacterial conversion. No established crab, shrimp, clam or other bottom fishery exists in the area so that little of this biomass is removed. If 70 g/m^2 of phytoplankton grazed by the fish annually is accepted as a reasonable estimate, then fish consumption amounts to roughly half of the total phytoplankton production.

Unfortunately, Trevor Channel is not representative of all of Barkley Sound. Instead it benefits more directly from upwelling off the entrance to Juan de Fuca Strait and fresh water inflow from Alberni Inlet. Thus it is expected to be more productive than the northern part of Barkley Sound. It has been pointed out, on the other hand (Hourston, personal communication), that the herring juveniles concentrate on the southern shores of Barkley Sound. Hence unevenness in regional distribution of plankton feeders compensates for the regional variation in productivity.

It is of interest to compare the productivity computed for Trevor Channel with that determined elsewhere from observations on the natural environment. Table II shows the productivity with methods of determination in diversified regions of the world. An examination of the figures suggests that the productivity calculated for Trevor Channel is comparatively low. Judging from the relatively large existing fishery in the area and the large nutrient concentrations, it might be assumed that the productivity is far greater than evaluated here. If an upper

TABLE II.—Productivity of Trevor Channel and other marine regions from chemical measurements.

Location	Productivity as carbon	Observations used	Reference
	g/m²/year		
Trevor Channel[a]	56	Oxygen depletion and fishery statistics	Present paper
Trevor Channel[a]	62	Phosphate liberation and fishery statistics	Present paper
Puget Sound[b]	30–111	Phosphate depletion	Waldichuk and Gould, 1953
Western North Atlantic 3–13° N	278	Oxygen depletion	Seiwell, 1935
Off Southern California	215–430	Oxygen depletion	Sverdrup and Fleming, 1941
English Channel	84	Phosphate depletion	Atkins, 1923
Barents Sea	170–330	Phosphate depletion	Kreps and Verjbinskaya, 1930
Hango (The Baltic)[c]	24	Phosphate depletion	Buch, 1952
Long Island Sound[d]	138–350	Phosphate depletion	Riley, 1941a
Gulf of Maine[d]	270	Phosphate depletion	Riley, 1941b

[a]Minimal values based on one cycle of nutrients during the year.

[b]Minimal value determined from maximum phosphate in February and minimum phosphate in July for different depths of euphotic zone off Point Jefferson (47° 45′ N; 122° 25′ W).

[c]Minimal quantity from beginning of rapid diatom outburst, 21 March, to maximum bloom, 21 April.

[d]For whole year with nutrients used several times.

limit of five times the value given in this work is chosen, the productivity would be about 300 g. per year as carbon. This is of the same order as the upper limit in Long Island Sound and the Barents Sea, which should be comparable. It can be concluded, therefore, that values computed here are an absolute minimum. Regeneration of nutrients in the upper layer, replacement of deep water more than once per year, and a continuous replenishment of nutrients in the euphotic zone by diffusion and/or advection from the deep water would all tend to increase the calculated productivity. More reliable results must await a seasonal study of the various processes involved with particular emphasis on the rate of supply of nutrients to the euphoic zone and their regeneration.

SUMMARY

Observations of the distribution of physical and chemical properties in Alberni Inlet and Trevor Channel in September have been made. The inlet system is characterized by extreme stratification in salinity and temperature near the surface during this time of year. Deep water originating from intermediate depths of the Pacific Ocean tends toward homogeneity in salinity and temperature, but exhibits a high phosphate concentration, low dissolved oxygen and low pH near the bottom. This is primarily a result of the bacterial action of decomposition. Low phosphate concentrations, high dissolved oxygen and high pH occur in the upper layer. Surface water owes its characteristics to dilution by runoff, heating by insolation, and phytoplankton proliferation.

Oxygen depletion and phosphate regeneration in the deep water have been used for the evaluation of productivity in Trevor Channel. Assumptions were made that the deep water is renewed once per year and that characteristics observed during the September survey were representative of those just before renewal. A correction was applied for the removal of plankton by the fish fauna. This amounts to as much as that computed from chemical measurements. The extent of regeneration of nutrients in the surface layer is unknown and has been neglected in the computations. An annual productivity of 56 g/m^2 from oxygen depletion and 62 g/m^2 from phosphate regeneration has been evaluated. These are minimal values because basic assumptions are probably not fulfilled.

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Spoilage of Fish in the Vessels at Sea: 2. Treatment on the Deck and in the Hold[1,2]

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ABSTRACT

A study has been made of some of the factors affecting the spoilage rate of fish in the trawlers at sea. It was found that two conditions were major causes of accelerated spoilage: (1) Treatments that resulted in very heavy initial contamination such as storing the fish directly against the slimy wooden pen boards, and (2) Treatments that resulted in a rise in the temperature of the fish. This latter may be a larger increase in temperature for a short period, such as exposure of the fish on the deck during warm summer weather, or a smaller increase over a longer period, such as results from inadequate or inefficient icing.

Other types of carelessness and unsanitary conditions did not have any significant effect on the fish until at least 6 or 7 days, as long as they were well iced during the subsequent storage period in the hold.

INTRODUCTION

Spoilage of gutted fish in the vessels at sea is chiefly of microbial origin. Any factor that adds to the number of microorganisms on the fish, or increases the growth and multiplication of those already present, contributes to the subsequent spoilage. Obviously, therefore, during the handling of the fish in the nets and on the deck, and later during stowage in the hold, there are many different factors such as contamination from contact with dirty surfaces, improper gutting or washing, over-exposure on the deck, careless or insufficient icing, and various forms of physical mistreatment of the fish, that may affect the spoilage rate.

The quality of the fish at the time of discharge is the result of a combination of all these factors. But all are not equally important. Experiments conducted at this Station prove beyond all doubt that insufficient or improper icing is one of the major causes of loss of quality at sea. If, for any reason, the temperature of the fish is allowed to increase beyond a certain point, the spoilage bacteria multiply rapidly, and invariably the fish spoil. There is no need for further experimental evidence to show the importance of time and temperature in the spoilage of fish. But the relative importance of some of the other factors was not so well known. The study of some of these other factors was the purpose of the work described in this paper. And as far as possible the results were obtained from experiments with fish caught and handled under conditions as they normally exist on a typical trawler fishing out of Halifax.

EXPERIMENTAL METHODS

The criterion of spoilage and the standards adopted were those suggested in a preceding paper by Castell and Triggs (1955), and consisted of a combina-

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[2]The preceding paper in this series appeared in **12**(3): 329–341 of this Journal (1955).

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tion of an organoleptic examination and the trimethylamine value[3] of the freshly cut fillet.

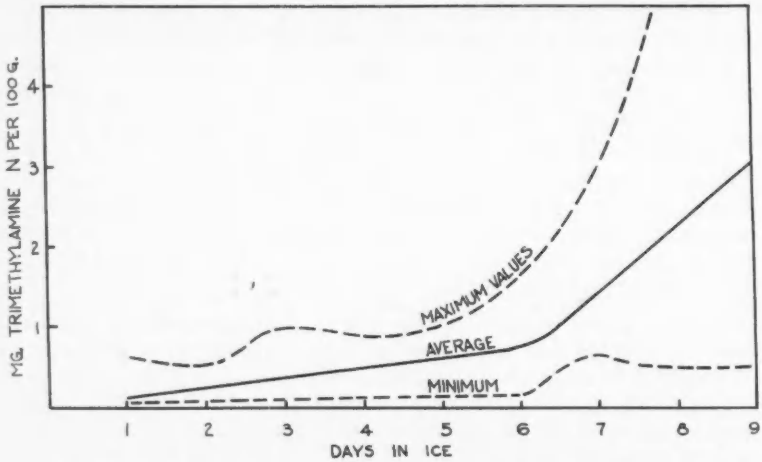
In order to arrive at some approximation of the importance of some particular treatment, similar fish, caught at the same time, were divided into two lots. One lot was used as a control; the second lot was exposed to a specific treatment or mistreatment, but otherwise carefully handled throughout. None of the fish used for testing various treatments on the deck were iced down in the pens in the normal manner, except where it was done for a definite purpose. Instead, most of the fish were very carefully iced in large fish boxes and then carried into the hold. This was done to avoid complicating the deck treatments by the variations that might occur subsequently during stowage in the pens.

EXPERIMENTAL RESULTS

Standard Trimethylamine Curve for Gutted Haddock Iced in Boxes

Before any specific mistreatment on the deck was examined, an attempt was made to obtain a spoilage curve for fish as they are now normally handled on the deck. To do this, fish in groups of six or eight were taken from the boat's normal catch just as they were about to be lowered into the hold.

These were carefully iced in the same large fish boxes that were used for stowing the experimental fish, and stowed in the hold. During a period of several months, trimethylamine values were obtained for 263 of these fish that had been stored for 1 to 9 days in ice. From the accompanying figure it can be seen that a



Spoilage curve of the muscle in gutted haddock as indicated by 263 trimethylamine determinations made on freshly excised fillets immediately after the fish had been discharged from the vessel. These all received only the normal treatment usually given to the fish on the deck by the fishermen.

[3]In this series of papers, "trimethylamine value" indicates milligrams of trimethylamine nitrogen per 100 g. of fish.

typical trimethylamine curve was obtained. There was a gradual increase for the first 6 or 7 days, followed by a much steeper incline. If any factor in handling or treatment of the fish on the deck is to affect the keeping time of the fish significantly, one would expect a shift in the point where this change in the slope occurs. Therefore, in addition to the control tests made with every set of experiments, it is possible also to compare the results with a curve obtained from the ordinary treatment given the fish on the deck.

I. Treatment on the Deck

(1) *Washing the Fish after Gutting*—During five trips to sea, fifteen lots of fish were each divided into two groups; one group of each lot was iced down immediately after gutting without being washed or rinsed, the second group of each lot was washed by the fishermen in their usual manner. These fish had been in ice on the boat from 2 to 7 days at the time of landing. Organoleptically, fillets from even the oldest fish were in a reasonably good state of preservation at the time of examination, and there was nothing to distinguish between those cut from the washed and unwashed fish. The pH and trimethylamine values (Table I) also showed no difference as the result of washing or not washing.

Table I.—The average trimethylamine and pH values for freshly cut haddock fillets from fifteen lots of fish, half of which had been thoroughly washed and half not washed, after being gutted at sea. These fish were from 2 to 7 days in ice on the boat and stored in boxes.

Days in ice	Trimethylamine value[4]		pH[4]	
	Washed	Unwashed	Washed	Unwashed
7	2.5	1.5	6.6	6.6
7	1.1	1.1	6.5	6.6
6	1.1	1.1	6.6	6.6
6	0.8	0.7	6.5	6.5
6	0.6	0.7	6.5	6.5
6	0.4	0.3	6.5	6.6
5	1.1	2.0	6.4	6.3
5	0.7	0.8	6.4	6.4
5	0.4	0.4	6.4	6.4
5	0.3	0.2	6.5	6.5
4	0.5	0.7	6.5	6.6
3	0.7	0.7	6.4	6.5
3	0.6	0.5	6.4	6.6
2	0.3	0.3	6.5	6.5
2	0.1	0.4	6.4	6.5

[4]Each figure represents an average value obtained from testing six to eight fillets.

These results could simply indicate that the methods used by the fishermen to wash the fish were very inefficient, and that perhaps if the fish were more thoroughly washed with good clean water, the results might be different. Therefore on several trips fish were more thoroughly washed in clean, running sea water; others were left unwashed; and a third group was washed in water that was purposely contaminated with guts and slime. Once again (Table II) the differences in pH and trimethylamine were not very significant. It is interesting to note, however, that of the fish that had been stored 7 days in ice, those washed

Table II.—Trimethylamine and pH values of haddock fillets taken from fish that had been washed in clean water, contaminated water and not washed at all, prior to icing aboard the vessel. This was repeated on 3 days, giving fish that had been stored 3, 5, and 7 days in ice.

Treatment	Days in ice	TMA (Average)		pH (Average)	
Clean water	7	1.50	1.82	6.7	6.55
“	7	3.51		6.5	
“	7	1.54		6.5	
“	7	0.75		6.5	
Dirty water	7	2.80	2.79	6.7	6.66
“	7	3.07		6.5	
“	7	1.80		6.6	
“	7	3.29		6.6	
Not washed	7	1.78	1.26	6.6	6.60
“	7	1.12		6.6	
“	7	1.07		6.6	
“	7	1.07		6.6	
Clean water	5	0.54	0.92	6.3	6.42
“	5	0.96		6.6	
“	5	1.20		6.5	
“	5	0.98		6.3	
Dirty water	5	0.75	0.88	6.6	6.45
“	5	1.88		6.6	
“	5	0.68		6.3	
“	5	0.21		6.3	
Not washed	5	0.64	0.97	6.4	6.40
“	5	0.95		6.4	
“	5	0.30		6.5	
“	5	2.00		6.3	
Clean water	3	0.74	0.67	6.5	6.40
“	3	0.59		6.4	
“	3	0.59		6.3	
“	3	0.75		6.3	
Dirty water	3	0.76	0.75	6.5	6.50
“	3	0.83		6.5	
“	3	0.45		6.5	
“	3	0.98		6.5	
Not washed	3	0.39	0.56	6.6	6.55
“	3	0.53		6.6	
“	3	0.85		6.5	
“	3	0.48		6.5	

in the dirty water were slightly inferior. The fillets from these fish were slightly softer and were beginning to develop off-odours. However, there was little to choose between those washed in clean water and those not washed at all.

Because of the possibility that washing might actually be the means of grossly contaminating the gut cavity, further experiments were carried out in which the fish were washed before gutting and compared to fish washed in the usual manner, and to others not washed at all. These fish were all iced down for 6 days; once again they showed no significant differences as the result of the treatment given.

Subsequent to these experiments, which were all carried out on one particular trawler, opportunities developed for further tests on the effect of washing fish in other boats. These included experiments which varied in size from ones involving full pens of fish down to those in which 25 to 30 fish were stored in large boxes. The result is that more data have been accumulated on the effect of washing than for any other phase of treatment or mistreatment of the fish on the vessels.

The results were not always the same. In some tests the unwashed fish were less uniform in quality than those which had been washed. This was particularly noticeable in regard to the development of surface slime. In other tests the fish washed before gutting kept a little longer than those washed after gutting. In still others there was no apparent difference in the spoilage rate of washed and unwashed fish, or whether they were washed before or after gutting. In no instance did the effect of washing or not washing, or washing before or after gutting, become apparent before 6 days in stowage; more frequently it was not until after 7 or 8 days.

Although these later experiments added very little to the picture, they did focus attention on another closely related problem; that is, variations in the extent to which the fish are contaminated by the fishermen during the gutting. After removing the intestines and other internal organs from the incised gut cavity, the fisherman thoughtlessly (or perhaps for want of more space) tosses them back onto the remaining ungutted fish. As more and more fish are gutted, those remaining in the checkers receive an increasing amount of this offal. This gross contamination is in addition to that of the faeces that are normally pressed out of feedy fish under pressure.

So far, only a few tests have been made comparing the keeping time of relatively uncontaminated fish from the top of the pile with those which remain at the bottom after the majority have been removed and gutted. The preliminary results with these grossly contaminated fish have indicated greater differences in keeping time than were obtained between other fish that were washed or not washed after gutting. Once again, however, it was noted that the difference in the spoilage rate of these grossly contaminated fish did not show up in carefully iced fish until after they had been in storage for more than 6 days.

(2) *Bruising and Crushing on the Deck*—Severe bruising of a freshly caught live fish usually results in bloody discoloration of the muscle. The bruising in the particular tests carried out in this work occurred in the checkers on the deck and in every instance the fish were dead. Under these conditions no blood spots or haemorrhages were observed.

These fish were tagged and then purposely kicked about and trampled by the fishermen with their rubber boots. It is not possible to give a measure of this mistreatment, but it was as severe as could ordinarily happen to fish during normal fishing operations.

The results were not always consistent, perhaps because the treatment, or mistreatment, was not uniform enough. From the appearance of the fillets, it would seem that in the more severe mistreatments, the surface spoilage organisms were able to gain direct access to the muscle beneath the skin. In these cases

there was a more or less localized spoilage area and a slightly higher trimethylamine value for the whole fillet. Where differences in odour and trimethylamine values did occur as a result of bruising, they could be distinguished only after the fish had been held in ice for at least 6 or 7 days. After that period, most of the bruised fish deteriorated much faster than the controls (Table III).

TABLE III.—Trimethylamine and pH values for fillets cut from seven lots of crushed and carefully handled haddock which had been stored in ice on the boats from 3 to 7 days.

Days in hold	Trimethylamine		pH	
	Control	Crushed	Control	Crushed
3	0.19	0.38	6.3	6.3
4	0.87	0.56	6.4	6.7
4	0.20	0.31	6.3	6.4
5	0.61	0.46	6.7	6.7
6	0.27	0.57	6.5	6.4
6	0.90	1.20	6.8	6.9
7	1.30	1.56	6.8	6.9

(3) *Improper Gutting*—Two specific faults frequently were observed in the gutting of the fish. The first fault was the failure to remove the last few inches of the intestine, which remained attached to the vent. In "feedy" fish this often resulted in the development of a decidedly obnoxious faecal odour in the gut cavity, and a similar off-odour in that part of the fillet near the anus in the gutted fish. Frequently this developed into a type of spoilage very similar to the characteristic "bilgy" condition that occurs when fish are jammed tightly against the wooden walls or pen boards of the vessel. There appeared to be no relationship between this type of spoilage and a rise in either pH or in the amount of trimethylamine that had developed. It was observed frequently that haddock fillets had this particularly offensive faecal odour with trimethylamine values of less than 1.0 mg. per 100 g. and pH values ranging from 6.5 to 6.7.

The other fault in gutting was the extension of the knife cut beyond the vent and into the muscle. Fillets from these fish were softer, discoloured, and had an unpleasant odour in the portion of the muscle exposed by the cut. In contrast to the defect preyiously described, the pH of the affected area was frequently 0.4 or 0.5 pH unit above that of the remainder of the fillet. And the trimethylamine values were also considerably above normal.

Once again, where reasonable care was taken in icing the fish, the results of these defects rarely became noticeable in the fillets until after the fish had been stowed for 6 or 7 days. In one particular trip, during which the oldest fish were in ice 7 days at the time of landing, fish were purposely left each with a small portion of the intestine in the gut cavity. Special care was taken to ice these fish well. It was impossible to distinguish fillets cut from such fish from those cut from normal fish stowed the same length of time in ice.

In still another test, fish with and without small portions of the intestine were tagged and iced down in the pens by the fishermen in their usual manner. These fish were in the hold for only 6 days but were not well iced. Representative

fillets were examined from both groups by persons unacquainted with the history of the fish. They noted that the fillets from the fish retaining a portion of the intestine were extra well trimmed, an indication that the filleter had removed discoloured tissues. Furthermore, in spite of this extra trimming, these fillets were slightly discoloured and smelled mildly faecal in this area.

(4) *Exposure on the Deck*—When large numbers of fish are allowed to pile up on the deck, the initial deterioration in quality may take place from several different causes. When such a condition exists for 6 or 8 hours or more, especially on a rolling sea, the fish at the bottom of the pile often appear messy and crushed. These bruised and softened fish are frequently discarded by the fishermen at the time of gutting. During the summer time the bottom fish in the pile may be in direct contact with previously heated deck surfaces. There is also the problem of contamination from faeces that are squeezed out from the fish under pressure. And lastly, there is the increase in the temperature of the fish during the period when they are on the deck without ice for hours at a time, and often exposed to bright sunshine.

In the following tests the fish on the top of the pile, exposed to the sunshine and the atmosphere, were studied. There are a number of variables even with these top fish: the season of the year, the time of day, and the atmospheric conditions such as temperature, sunshine, fog, or rain. It was next to impossible, in the time available, to control all the variables, so a series of tests was conducted comparing the exposed and unexposed fish under a variety of conditions (Table IV). It can be seen that during the cool weather in May, exposure for

TABLE IV.—Trimethylamine and pH values of cod and haddock fillets from fish that had been exposed on the deck at various times, and under various conditions, together with values for similar fish caught at the same time but not exposed on the deck.

Date	Hours exposed	Sun-shine	Air temp.	Type of fish	Days in hold	Trimethylamine		pH	
						Exposed	Controls	Exposed	Controls
			(°C.)						
May 19	2	+	5	Cod	3	0.40	0.38	6.5	6.5
"	4	+	5	Cod	4	0.36	0.46	6.7	6.6
"	7	−	3–5	Cod	7	0.85	0.91	6.7	6.6
June 6	3	+	15	Cod	5	1.30	0.66	6.8	6.7
July 7	5	±	15	Cod	5	1.19	0.55	6.7	6.5
June 6	5	+	14	Had.	6	1.12	0.47	6.5	6.6
" 7	5	+	13	Had.	5	1.40	0.45	6.7	6.4
July 14	2	+	21	Had.	6	0.61	0.40	6.4	6.4

2 or 4 hours during the day time, or for even 7 hours during a cloudy afternoon and evening, had little or no perceptible effect on the fish. During June and July, exposure for 3 to 5 hours did become significant. In only one of the five tests made during the summer were the results negative or of doubtful significance, and in this case the fish were exposed for 2 hours only.

Many of the fillets from the exposed summer fish were much softer than their corresponding controls, and incidentally, their subsequent spoilage was much more rapid. Is this softening a purely physical phenomenon, resulting from the effect of heat on the muscle proteins, is it a softening that generally

accompanies bacterial action on the fish muscle, or is it due to autolysis? At this Station, well iced, one-day-old haddock were exposed from 5 to 30 minutes under the direct rays of infra-red lamps and then stored again in ice for 4 days. When the fish were examined, those that had been exposed to the heat rays appeared to be slightly softer to the touch. But when the fillets were cut out and compared, independent judges were unable to identify the heat-treated fish from the controls. Thirty minutes under a treatment that raised the muscle temperature to 20°C. (68°F.) produced nothing comparable to the softness resulting from fish exposed for several hours on the deck in summer sunshine.

Not too many conclusions can be drawn from these limited experiments, subject to so many variables, but it seems obvious that exposure on the deck for more than 2 hours during the warm weather is decidedly detrimental to the fish.

Four procedures in handling the fish on the deck have now been examined, which, if not properly carried out, are considered to have an adverse effect on the time the fish will keep. The results have not been very striking. With the possible exception of exposure on the deck during warm weather, none of these mistreatments appeared to be a major cause of rapid deterioration of fish in the boats. When exaggerated, or carried to the extreme, badly bruising the fish or washing them in very dirty water might reduce the keeping time by a day or so; carelessness in gutting may hasten the spoilage of a certain percentage of the fish, especially those stored for longer periods. On the other hand, there is little evidence to indicate that extreme care in gutting, washing, and handling the fish on the deck adds very much to the normal keeping time as they are now handled at sea. Some factors, other than those already examined, apparently determine the point where the spoilage curve turns sharply upward.

II. Treatment of Fish in the Holds

Once the fish are iced down in the pens, they remain untouched until the boat is ready for discharge at the wharf. Any factor during this period that accelerates spoilage must do one of two things. It must add relatively large numbers of psychrophilic bacteria to the fish, or it must speed up the multiplication of those already present. The problems, therefore, of spoilage during stowage at sea can be pretty well limited to the effect of sanitation on the initial extent of contamination, and to the effect of temperature on the growth rate. A related factor is the crushing effect of large amounts of fish not properly supported by shelves.

(1) *Care in Icing*—Previous laboratory tests with both fillets and gutted fish have shown that a reduction of a few degrees in storage temperature in the range immediately above freezing may double the keeping time of fish (Castell and MacCallum, 1950). We also know that there is considerable variation both in the rate of cooling and the ultimate temperature of the fish in our trawlers at sea (MacCallum *et al.* 1949). The rate of cooling is chiefly associated with the proper mixing of the ice and fish. Fishermen frequently pile their fish in layers 15 to 18 inches (38 to 46 cm.) deep, interspersed with thinner layers of

ice. The fish in the centre of these deep layers often require 24 to 36 hours to cool down to near the temperature of the ice.

When insufficient ice is used, or when there are serious heat leaks through the skin of the vessel or the walls of the pens, it has been shown that the fish may never get below 3 to 5°C. (37 to 41°F.).

The first tests were to check on the efficiency of the icing procedures as ordinarily carried out by the fishermen. To do this, similar lots of haddock, cod, and flounder were each divided into two groups. One group of each lot was iced down in large fish boxes, with special care taken to see that the ice and the fish were intermixed properly. The other group of each lot was iced down in the pens by the fishermen who took no special care to mix the ice and the fish, nor to distribute the ice evenly in the pens. In order to avoid complicating the tests by additional spoilage factors, none of the fish from these pens were taken from positions immediately adjacent to the walls or pen boards, or from the bottom section of the pen.

The results of these tests are seen in Table V. In every instance the carefully iced fish in the boxes were in a better condition than the corresponding fish from the pens.

TABLE V.—Comparison of haddock carefully iced in large boxes with similar fish iced by the fisherman in the pens, where less care was taken to mix the ice and the fish properly.

Container	Fish	Days in ice	Number of fish tested	Average TMA	pH		
					Average	Minimum	Maximum
Boxes	Cod	4	20	0.53	6.6	6.2	6.8
Pens	"	4	24	1.20	6.8	6.6	7.0
Boxes	Flounder	7	13	0.56	6.3	6.0	6.8
Pens	"	7	15	4.50	6.8	6.6	7.0
Boxes	Flounder	8	13	0.83	6.5	6.2	6.7
Pens	"	8	18	5.40	6.8	6.7	7.0
Boxes	Haddock	6	21	0.72	6.5	6.4	6.6
Pens	"	6	27	5.80	6.8	6.6	7.0

The test was repeated, using haddock, but this time special care was taken to see that the fishermen did a more thorough job of mixing the fish and the ice in the pens. The result was that the fish in the pens were very much better than in the preceding experiments and the fillets cut from them could not be distinguished by organoleptic examination from the fillets cut from fish stowed in the boxes (Table VI).

(2) *Effect of Pen Shelfboards*—In most Canadian Atlantic trawlers there are sixteen fish pens, eight on either side of a centre alley-way. Each pen is divided into three sections, or levels, by inserting two sets of shelf boards. A full pen may hold up to 8,000 or 10,000 pounds of fish and ice. The purpose of the shelf boards is to lessen the crushing effect of this weight on the bottom fish. Occasionally the practice is to fill the pens 8 to 10 inches above the brackets on which the shelves rest, and then to insert the shelves. The explanation given

TABLE VI. — Comparison of haddock stored in boxes with similar fish in the pens where care was taken to thoroughly ice the fish.

Container	Days in ice	Average	
		Trimethylamine	pH
Boxes	1	0.40	6.4
Pens	1	0.19	6.3
Boxes	3	0.42	6.5
Pens	3	0.51	6.5
Boxes	5	0.68	6.6
Pens	5	0.82	6.6
Boxes	7	1.13	6.7
Pens	7	2.03	6.8

by the fishermen is that when the ice melts and the fish settle, the shelf comes to rest on the bracket. As a result of such practice the fish at the bottom may have the weight of the whole penful pressing down on them for 24 hours or possibly longer. However, unless the fish are very abundant, this circumstance may not often occur, because usually the lower sections are filled before starting on the middle and top sections.

Obviously, fish stowed at the bottom of a full, unshelved pen are severely crushed and may lose considerable weight. This has been shown by tests made at the Torry Research Station at Aberdeen, Scotland (Cutting 1951). This particular phase of the problem was of no concern in the following tests. The object was simply to determine whether the presence or absence of shelf boards made any considerable difference in the spoilage rate of fish as judged by the state of preservation of the fillets. To do this, similar pens were used on the opposite sides of the vessel. For six trips at sea, three additional shelves were inserted in one of the pens, giving six sections compared with the normal three in the control pen. On a subsequent trip the difference was made even greater by using six sections in one side and removing all the shelves from the other pen. Similar fish, caught at the same time, were iced down in these particular pens. Care was taken when selecting the samples to be tested, to see that they were taken from the corresponding location of the same section in each pen. Table VII gives the average, maximum, and minimum trimethylamine value for ten fish from the same location near the bottom of the pens having the two and five sets of shelf boards. The table shows no consistent differences in the trimethylamine values of the fish from these pens. Fish taken from two upper sections of these pens gave the same results. Examination of the fillets for spoilage odours showed no consistent difference. But there was a difference in the texture of the fillets. Those from the fish taken from the bottom sections of the pens with only two shelves were noticeably softer. Table VIII gives a more complete picture showing what happened when the shelves in one pen were omitted altogether. As would be expected, there was no difference in the fish in the upper portion of the pen. At the bottom, once again it was the texture of

TABLE VII.—Trimethylamine values of haddock from the bottom level of pens having five and two sets of shelf boards. Similar fish, caught at the same time, were used in both pens on each test trip.

Days in ice	Trimethylamine values					
	With 5 shelves above			With 2 shelves above		
	Average[5]	Minimum	Maximum	Average	Minimum	Maximum
9	3.9	2.9	5.1	2.2	0.9	2.6
7	2.4	1.0	3.3	1.7	0.9	2.6
7	2.0	1.2	3.3	2.8	1.1	4.9
7	1.2	0.4	2.2	1.5	0.4	3.1
6	2.1	0.7	3.6	1.6	0.8	2.9
6	1.3	0.5	2.4	2.1	0.7	4.7

[5]Each figure represents an average of ten fish taken from the same location in each pen.

the fillets that was most affected by the absence of shelving. This was very evident in the physical condition of the gutted fish as they were being discharged from the boat. Those at the bottom of the shelfless pen were badly crushed, soft, and mis-shapen.

TABLE VIII.—The effect of shelving on the quality of haddock stored in pens, as indicated by the trimethylamine, pH, odour, and texture of the fillets cut from the fish. Each figure represents an average of six fish taken in each of the locations given. The pen on the starboard side had five shelves, giving six levels. The pen on the port side had no shelves. The location of the fish on the port side is given in relation to where the levels would have been had the shelves been used.

Days in ice	Position in the pen	Average, minimum and maximum TMA		pH		Odour		Texture	
		Starbd.	Port	Starbd.	Port	Starbd.	Port	Starbd.	Port
		(mg. per 100 g.)							
5	centre of top level	1.0 (0.6–1.47)	1.8 (0.8–2.5)	6.4	6.5	none	none	firm	firm
5	centre of 3rd level	1.3 (1.0–1.6)	0.9 (0.7–1.0)	6.5	6.5	very slightly off	none	slightly soft	slightly soft
5	centre of 4th level	1.9 (1.2–2.4)	1.2 (0.6–2.3)	6.4	6.6	none	none	slightly soft	soft
6	centre of 5th level	2.2 (1.5–2.8)	1.2 (0.6–2.1)	6.6	6.5	sour	none?	slightly soft	soft
7	front centre of bottom level	2.2 (0.9–3.1)	1.6 (1.0–2.4)	6.6	6.5	slightly sour	very slightly sour	slightly soft	soft
7	back centre of bottom level	3.2 (2.0–3.4)	3.1 (2.4–4.1)	6.5	6.6	sour	sour	soft	very soft

(3) *Location of the Fish in the Hold*—In theory, properly chilled fish that are completely buried in ice should all be at the same temperature. The only variables resulting from location in the hold should be differences in the amount of pressure on the fish and differences in the flow of melting ice water and fish juices through the pen. In actual practice it is much more complex than this, because the fish are not all properly chilled and iced. MacCallum *et al.* (1949) have already shown that heat leaks and inefficient icing methods do result in relatively large variations in the temperature of the fish during stowage.

To begin with, experiments prove that the fish are *not* always protected

properly from the contaminated wooden surfaces of the pens by a layer of ice. Work by Castell and Triggs (1955), Castell (1954), and MacCallum (1955) showed that this lack of protection from such contamination results in the previously mentioned very obnoxious type of spoilage commonly known as "bilgy" fish. The seriousness of this type of spoilage is so great it would appear needless to make further tests at this time to demonstrate its relative importance.

Fish may be located in the top, the middle, or bottom section of each pen, or they may be in the top, the middle, or bottom of each section. They can also be close to the walls and the pen boards or in the centre of the mass of ice and fish. It would take years to make a thorough study of this phase of the work.

Several hundred comparisons have already been made, taking six fish at a time from each individual location. The difficulty was to get the fishermen always to put similar fish, caught at the same time, in the locations under examination. However, an example shows the type of results that have been obtained.

One pen was completely filled with fish caught on the same day. At the time of discharge these fish were all 7 days in ice. Table IX gives the results,

TABLE IX.—The average trimethylamine and pH values and the odour from fillets cut from fish that had been in various locations in one hold for 7 days.

Position in pen	Average		Odour
	Trimethylamine	pH	
Top front of top section	1.2	6.5	Slightly sour
Bottom front of top section	1.5	6.6	Slightly sour
Bottom back of top section	2.4	6.5	Slightly sour
Top front of middle section	1.1	6.6	Not much odour
Bottom front of middle section	1.7	6.6	Not much odour
Bottom back of middle section	1.7	6.6	Slightly faecal, and sour
Top front of bottom section	1.6	6.6	Slightly sour
Bottom front of bottom section	2.5	6.6	Slightly sour
Bottom back of bottom section	2.2	6.7	Strong sour and slightly faecal

which are typical of many similar tests. In general, other things being equal, the following observations held:

(a) The fish in the lowest section deteriorated more quickly than those above.

(b) Within each individual section those at the bottom spoiled faster than those in the middle or at the top.

(c) Fish at the back of the pen spoiled faster than those at the front. In some instances, fish close to the side walls spoiled faster than those in the centre.

These observations refer only to fish that had not been jammed up against the boards at the sides and back of the pen. If the ice melts and the fish come in direct contact with the wooden surfaces, spoilage becomes much more rapid.

Over a period of several months 800 fillets from freshly cut haddock were examined for spoilage odours and trimethylamine values. Of these, 232 were

taken from the bottom section of the pens while the remaining 568 were from the two upper sections. Table X gives a comparison of these results. For the first 5 days, the fish from the bottom section appeared to be as good or better than those from the upper sections. After 6 days, the fish in the bottom had a higher mean trimethylamine value and a greater proportion were developing noticeable spoilage odours.

TABLE X.—Comparison of the quality of fillets cut from 232 haddock that had been from 4 to 9 days in the bottom section of a pen, with fillets cut from 618 similar fish taken from the two upper sections of the pen.

Days in the hold	Per cent of fish from bottom level	Mean trimethylamine values				Difference between means	Per cent fillets with spoilage odours	
		Bottom level	S.D.[a]	Upper levels	S.D.[a]		Bottom	Upper
4	21	0.60	...	0.69	...	−0.09	0	13
5	5	0.51	...	1.16	...	−0.65	0	38
6	18	1.49	0.013	1.16	0.055	+0.03	60	22
7	40	2.00	0.105	1.71	0.070	+0.29	45	47
8	34	2.42	...	1.47	...	+0.95	66	34
9	54	3.71	0.342	2.94	0.293	+0.78	100	100

[a]Standard deviation.

In icing experiments in the pilot plant at this Station, it was also observed that the fish at the bottom of a layer 14 inches thick had a slightly higher mean trimethylamine value and developed offensive odours earlier than those at the top. As these particular fish were surrounded by a layer of cracked ice one foot thick and were not under pressure, it would appear that the difference was not the result of temperature or pressure.

(4) *Sanitation in the Pens*—Most fishermen have learned from experience that fish placed directly against the wooden surfaces spoil more rapidly than those imbedded in ice. As a result of this experience, there is a general belief that care in washing the pen surfaces is one of the most important factors in controlling spoilage. As this is directly related to the production of bilgy fish, it is a problem of utmost importance.

Before the fishermen started to wash the pens after discharging their cargo, two pens directly opposite each other were selected for the first test involving pen sanitation. The pen on the starboard side was sprayed with a detergent, and scrubbed thoroughly with a stiff brush, care being taken to get into all the open cracks and corners. This was followed by a generous flushing with clean water, spraying with a hypochlorite solution containing approximately 1000 parts per million of available chlorine, and after 10 minutes again thorough rinsing with clean water. The corresponding pen on the port side was left just as it was when the fishermen discharged the cargo. It was slimy and malodorous. If the sanitation of the surface of the pen boards was a significantly important factor, there should have been a marked difference in the quality of the fish from these two pens. Sixty-four fish, taken in groups of four from various locations in the pens, were used for making the comparison.

As might be expected, fish from corresponding locations that were not in direct contact with the wooden surfaces were in approximately the same state of preservation from both the washed and unwashed pens. After 7 days in the hold, the trimethylamine values for fish in both pens ranged between 0.9 and 3.6 mg. per 100 g. Many of the fillets were becoming soft and were developing sour odours, but there was no perceptible difference in the condition of these fillets from each of the two pens. Every fish examined that had been in direct contact with the wooden surfaces, whether from the washed or unwashed pens, had decidedly bad odours. The fillets were characterized as "faecal", "skunky", and "bilgy." The fillets with the most offensive odour came from fish in the washed pen!

It must be remembered that these fish were all 7 days in the hold before being examined. An earlier examination might have shown the fish in the unwashed pens were developing these vile odours earlier than those in the washed pens. But further tests at this Station did not confirm this. Fish were iced down against washed and unwashed pen boards and examined periodically. Those against the washed boards developed decidedly bad odours just as quickly as those against the unwashed boards.

At first these results may appear contradictory to what has been found about the value of sanitation from very long experience. Actually, they are believed to show that it is almost impossible to make a significant reduction in the bacteria in soft soggy wooden boards that are impregnated with slime and fish juice, by merely washing or "sterilizing" their exterior surfaces. Counts on these washed and supposedly sterilized boards have yielded up to 50,000,000 bacteria per square centimeter.

(5) *Ice as a Source of Contamination*—Artificial ice, and even most natural ice, usually contain relatively small populations of bacteria. These range from a few dozen to a few hundred, and once in a while a few thousand, bacteria per gram. This refers only to the bacteria frozen in the ice. Contamination on the surface of the ice is quite a different story. This contamination comes from two sources:

The first source is from the sawdust, straw, or other materials used for insulating the ice in storage sheds. During the spring and summer, enormous populations of psychrophilic bacteria, chiefly *Pseudomonas*, are built up in the cool, damp, or soggy material close to the ice. Fortunately, it is a relatively simple job to overcome this contamination. If the ice is thoroughly washed before crushing, the film of dirt, straw, sawdust, and most of the accompanying bacteria, are removed. If this is not done, the fish may be iced down with ice carrying from a hundred thousand to half a million fast-growing fish-spoiling bacteria per gram. As the ice melts, these are washed down around the fish. Tests have shown that contaminated ice of this type not only lessened the keeping time of fish by several days, but also changed the predominating microflora, resulting in an entirely different type of spoilage. This, of course, applied almost wholly to natural ice.

The second source of contamination for both natural and artificial ice is the boat itself. Cracked and powdered ice stored in the fish hold of a vessel must necessarily come into intimate contact with the surface of all the walls of the pen. Furthermore, it is pressed into every crack and corner.

Skippers and plant foremen know what happens if the fish in the hold are pressed directly against dirty pen boards. Invariably they spoil rapidly. What then are we to expect if ice that has been pressed against such boards for several days is used directly on the fish? (See Table XI.) Pens should be cleaned

TABLE XI.—Bacterial counts, per gram, of ice used for chilling fish aboard trawlers taken before and at various periods after it has been blown into the hold.

Location of samples	Number of samples	Range of bacterial counts per gram	Average bacterial count per gram
On the wharf	18	50 – 40,000	9,500
Centre of pen immediately after loading	10	750 – 200,000	33,000
Against pen walls immediately after loading	10	10,000 – 900,000	280,000
Centre of pen of unused ice at end of trip	23	18,000 – 5,000,000	825,000
Against pen walls at end of trip	22	69,000 – 13,500,000	1,800,000
Dirty ice used on fish at end of trip	12	4,300,000 – 87,000,000	26,000,000

thoroughly if they are to be used for storing ice. As it is gradually removed from the storage pens, the portions against the wall boards fall down and are mixed in with the main body of the ice. If the ship rolls in a heavy sea, the changing pressure adds still more contamination by squeezing out gurry and slime from the cracks between the boards.

There is also the problem of the ice that has been left unused after each trip to sea. Some of the more thrifty fishermen feel that this ice should not be wasted, so fresh ice is piled on top. Sometimes this bottom layer of unused ice may remain in the boat for several months and then at some time or other, when no surplus of ice has been taken on board, it is finally broken up and used on the fish.

Of what significance is heavily contaminated ice to the keeping time of fish in the hold? So far only indirect evidence has been obtained. For example: At one particular plant only artificial ice was being supplied to the vessels. By a coincidence the supply of ice ran short and the regular man in charge of icing was replaced by a less experienced man. For several weeks he supplemented the small supply of artificial ice by a large proportion of ice cut from

a nearby lake and did not take the trouble to wash off the film of dirt and insulating material before putting it into the cracking machine. Cracked ice taken from the boat immediately before leaving for the banks had a load of 3 to 4 million psychrophilic bacteria per gram. The type of spoilage developing in the fish on this trip was organoleptically different from that of the previous trips. The spoilage of fillets cut from the fish was not only different to, but also more rapid than, that of fillets cut from corresponding fish previously taken from this vessel.

Some ice was taken from the boat before sailing for the Banks. Before it was completely melted, very lightly contaminated fillets were immersed in it for 20 seconds. The same was done with some partially melted artificial ice with a very low bacterial content. After 5 days at 0°C. (32°F.) the fillets which had been dipped in the melted unwashed natural ice were developing typical sour odours similar to those from the boat's catch. Those dipped in the ice water from the artificial ice spoiled differently and several days later. Pure cultures of the predominating bacteria in the contaminated ice also produced the characteristic type of spoilage when inoculated onto sterile fish muscle and incubated at 0°C.

DISCUSSION

Basically various ways of mishandling fish on the deck and in the hold can contribute to their subsequent spoilage by two closely related means. First, they can add to the number of bacteria on the fish by direct transfer from contaminated liquids and dirty surfaces. Second, they can provide an environment suitable for the multiplication and chemical activity of the bacteria already on the fish. Under the conditions as they now exist on our trawlers, temperature is by far the most important factor limiting bacterial growth.

Therefore, in assessing the relative importance to spoilage of the various ways of handling fish, primary concern is with either the number of spoilage organisms that are added by contamination or the effect of time and temperature on the growth and activity of those already present.

The relative importance of the extent of initial contamination compared with subsequent growth and activity differs under different circumstances. At relatively high temperatures, 15° to 25°C. (59° to 77°F.), multiplication is so rapid that, irrespective of initial contamination, the fish soon spoil. Even at 5° to 15°C. (41° to 59°F.), lightly contaminated fish rarely keep more than 1 or 2 days. Below 5°C. and more particularly between —2° and 0°C. (28.4° and 32°F.), the retarding effect of temperature on bacterial activity becomes increasingly important.

Where the initial contamination exceeds a million per square centimeter, the bacteria are already numerous enough to initiate spoilage, without requiring a period for further multiplication. It would appear that in at least one instance this condition exists; that is when the fish are pressed directly against the heavily contaminated, slimy, wooden surfaces in the hold. It is probable that a direct contamination of the fish with its own faeces would produce a similiar condition

of a heavy initial contamination. Here the spoilage rate is limited only by the activity of the spoilage enzymes.

In most other cases, further multiplication of the bacteria on the fish must occur before they are numerous enough to cause appreciable spoilage. To this another consideration must be added. Before the period of rapid multiplication, the bacteria go through a lag phase where their numbers remain almost stationary. Hess (1934) has shown that for *Ps. fluorescens* this period of retarded multiplication is increased from less than 1 day at 20°C. to 3 days at 5°C., 4 days at 0°C., and 6 days at —3°C. (26.6°F.). Jensen (1941) has also pointed out that with fresh meat, 3 or 4 hours at 26°C. (78.8°F.) before going into storage at 4.4°C. (39.9°F.) may completely eliminate this initial period of retarded bacterial growth that normally occurs at the storage temperature.

In the treatments dealt with in this paper, it was shown that care taken to prevent excessive contamination of the fish from their own faeces while in the checkers added about 2 days to the keeping time. It was also shown that fish pressed directly against the pen boards spoiled very rapidly. In both cases the fish started out with a microflora that was numerous enough to cause spoilage without any further increase.

Fish exposed on the deck for short periods at relatively high temperatures also had their keeping time reduced by 1 to 3 days. It would seem probable that this treatment not only started bacteria increasing rapidly, but also reduced the lag period when they were in storage in the hold.

In most other treatments involving increased initial contamination or the reduction of contamination, no effect was evident until the fish had been in storage in the pen for 6, 7, or 8 days at or near 0°C. Here the effect of low temperature is evident, both in increasing the lag period and in retarding growth during the accelerated phase.

To the uninitiated, the negative results that were obtained from washing the fish on the deck are rather perplexing. In general, washing improved the appearance of the fish by removing the superfluous blood and gurry, but added very little to the keeping time. Tests made at this Station with many types of washing machines have demonstrated the exceedingly difficult job of removing the bacteria-laden slime from fresh fish. It is very doubtful whether the "dunking" that fish generally receive in the wash box on the deck of the trawlers does more than remove excess blood and loose bits of slime and faeces. Some results suggest that at times even this advantage is more than likely offset by heavy contamination of the gut cavity during washing. Our conclusion, therefore, is that in practice the keeping time of the fish that are grossly contaminated in the checkers may be improved by washing; but that under most conditions the present methods of washing add little or nothing to the keeping time. These results are very similar to those obtained by workers at the Torry Research Station in Scotland who have concluded "the proper method of washing [fish] at sea has not yet been devised" (Cutting, 1954).

Pressing and crushing the fish in the pen through the lack of proper shelving, as might be expected, did not noticeably increase the microbial spoilage rate.

However, it was found that the crushed fish were soft, mis-shapen, and definitely inferior in appearance.

Certain areas in the pen seem to predispose the fish to more rapid spoilage. It would appear that at least three factors are involved here. Direct contact with wooden or other pen surfaces frequently leads to the bilgy type of spoilage. Apart from this, temperature appears to be the major factor. The places where fish spoiled most rapidly were the same pen locations where MacCallum (1949) found the fish had slower cooling rates. And still other experiments have suggested that seepage from above, plus improper drainage of the bottom fish, are also contributing factors.

The object of all this work is to be able to bring in better fish. The results obtained here suggest that further experimental work on the boats should include the following:

(*a*) A better arrangement for gutting the fish on the deck, so that the guts, faeces, etc. are not thrown back on the ungutted fish.

(*b*) Continuous washing of the round fish with a hose in the checkers before they are gutted, to remove excess faeces.

(*c*) Care in gutting to prevent rips into the muscle and to eliminate portions of the intestine being left in the gut cavity.

(*d*) Rapid handling of fish on the deck during warm weather to reduce their exposure to sunshine and high temperature.

(*e*) The addition of a bactericide or a bacteriostat to the wash water, or perhaps to the ice used for chilling the fish.

(*f*) Care in preventing the fish from coming in direct contact with the pen boards.

(*g*) And above all—care in seeing that the fish are rapidly chilled and held as close to 0°C. as possible throughout their stowage at sea.

SUMMARY

A study has been made of the effect on spoilage of haddock of various treatments that they receive on the trawlers at sea, with the following results:

(1) Except in the case of grossly contaminated fish from the bottom of the checkers, washing the gutted fish added little or nothing to the keeping time.

(2) Bruising or crushing the fish on the deck through careless handling produced inconsistent results, but in any case accelerated spoilage was never observed until the fish were at least 6 or 7 days in the hold.

(3) Carelessness in gutting, where the knife cut runs up into the fillet, or when bits of intestine are left in feedy fish, resulted in accelerated spoilage in the particular areas concerned, but only after the fish had been 6 or 7 days in ice.

(4) Exposure on the deck during warm summer weather softened the fillets and accelerated spoilage. In the cooler spring weather similar or longer exposure had little or no detrimental effect.

(5) Fish carefully iced in boxes kept much better than similar fish iced in pens by the fishermen. When special care was taken to ice the fish very thoroughly

in the pens the difference between the keeping time in pens and boxes became very much less.

(6) Crushing the fish as a result of inadequate shelving did not accelerate bacterial spoilage, but it did result in softer, inferior-appearing fish.

(7) Fish pressed against the wooden pen boards deteriorated rapidly. This was not prevented by washing the penboards.

(8) Even when well iced and kept away from the boards, fish at the bottom of the pens spoiled more rapidly than fish at the top.

(9) Ice, and more particularly natural ice that has not been washed before crushing, can add significantly to the spoilage bacteria on the fish. Ice blown into dirty pens can act as a carrier, transferring bacteria from dirty pen surfaces to the fish.

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Station List of the "Calanus" Expeditions, 1953-4[1]

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Fisheries Research Board and McGill University

"CALANUS" SERIES, NO. 10

ABSTRACT

A list is given of 89 stations where biological or oceanographic observations or collections were made by the *Calanus* in Hudson Bay, western Hudson Strait and Ungava Bay, during the 1953 and 1954 seasons.

INTRODUCTION

Two previous station lists of the *Calanus* expeditions have been published (*J. Fish. Res. Bd. Canada,* **9**: 65–82, 1952; *Ibid.,* **11**: 98–105, 1954) and include stations occupied from 1947 to 1952. Work was begun by the *Calanus* in Hudson Bay in 1953, and continued there and in western Hudson Strait and Ungava Bay during the 1953 and 1954 seasons. The positions of the 1953 and 1954 stations are shown on the accompanying map.

LIST OF STATIONS

Station	Map location	North latitude	West longitude	Depth (*metres*)	Type of station (work done)
1953					
501	Churchill Harbour, inner basin	58° 47′	94° 12′	1–7	Plankton, hydrographic
502	5 miles northeast of Churchill	58° 50′	94° 04′	22–27	Plankton, benthos (dredging and trawling), hydrographic
503	35 miles east of Tavani	61° 59′	91° 50′	64–91	Plankton, hydrographic
504	Chesterfield Inlet	63° 20′	90° 42′	0–7	Littoral, hand line and gill net fishing
505	Hydrographic section from Chesterfield to Southampton Island	63° 26′	89° 36′	100	Plankton, hydrographic
506		63° 31′	88° 39′	137	Plankton, hydrographic
507		63° 36′	87° 43′	146	Plankton, hydrographic
508	Hydrographic section from Southampton Island to Coats Island	63° 13′	84° 22′	95	Plankton, hydrographic
509		63° 04′	84° 03′	124	Plankton, hydrographic
510		62° 56′	83° 44′	137	Plankton, hydrographic
511	Coral Harbour	64° 08′	83° 08′	5–11	Benthos, hand line fishing
512	Fisher Strait	63° 27′	84° 08′	18–21	Plankton, benthos (trawling), hydrographic

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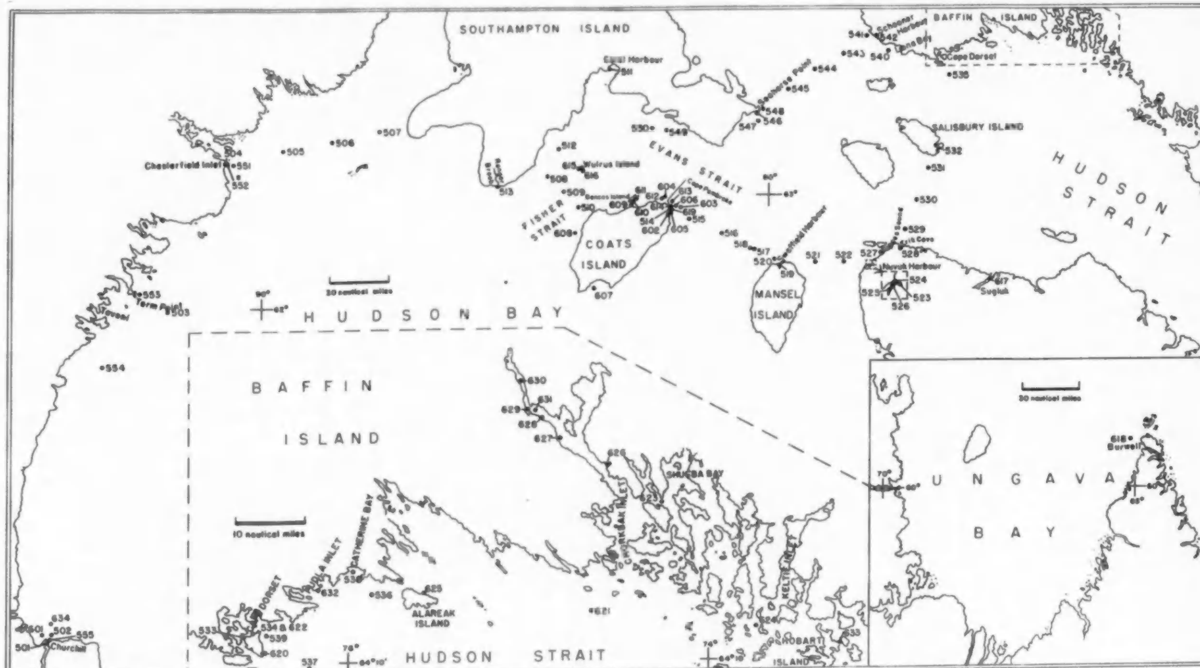
Station	Map location	North latitude	West longitude	Depth (*metres*)	Type of station (work done)
513	Mouth of Ranger Brook	63° 06′	85° 19′	0	Littoral
514	Northeastern Coats Island	62° 53′	81° 54′	0 7 9–10 20	Littoral Hand line fishing, hydrographic Benthos (dredging) Plankton
515	Hydrographic section from	62° 48′	81° 34′	137	Plankton, hydrographic
516	Coats Island to Mansel	62° 40′	80° 54′	219	Plankton, hydrographic
517	Island	62° 31′	80° 15′	238	Plankton, hydrographic
518	Near 517	62° 33′	80° 24′	230	Plankton
519	Swaffield Harbour, Mansel Island	62° 23′	79° 44′	0–9	Benthos, littoral, hand line fishing
520	5 miles north-west of 519	62° 27′	79° 51′	73–137	Plankton, benthos (dredging), hydrographic
521	Hydrographic section from Mansel Island	62° 25′	79° 02′	175	Plankton, hydrographic
522	to N.W. Quebec	62° 25′	78° 29′	107	Plankton, hydrographic
523	Nuvuk Harbour	62° 23′	77° 54′	18–20	Benthos, hand line and gill net fishing
524	Nuvuk Harbour	62° 23.5′	77° 55′	55–82	Benthos, long line fishing
525	Nuvuk Harbour	62° 22′	77° 58′	0–9	Littoral, hand line fishing
526	Nuvuk Harbour	62° 23′	77° 56′	50–53	Plankton, benthos (dredging)
527	Digges Sound	62° 28′	77° 47′	356–415	Plankton, hydrographic
528	Erik Cove	62° 32′	77° 24′	0–36	Plankton, littoral, hand line fishing
529	Hydrographic section from	62° 42′	77° 17′	420	Plankton, hydrographic
530	Erik Cove to Salisbury	62° 58′	77° 03′	220	Hydrographic
531	Island	63° 15′	76° 49′	183	Plankton, hydrographic
532	Salisbury Island	63° 27′	76° 43′	0–9	Littoral, benthos
533	1 mile west of Cape Dorset	64° 14′	76° 35′	12	Benthos, hand line fishing
534 & 622	Cape Dorset settlement	64° 14′	76° 33′	0–30	Plankton, benthos, littoral, hand line, long line and gill net fishing
535	10 miles south of Cape Dorset	64° 04′	76° 25′	140–155	Plankton, hydrographic
536	4 miles west of Alareak Island	64° 20′	75° 50′	—	Sealing
537	10 miles south-east of Cape Dorset	64° 08′	76° 12′	—	Sealing
538	Catherine Bay	64° 23′	75° 58′	—	Sealing
539	2 miles east of Cape Dorset	64° 14′	76° 28′	64–109	Plankton

Station	Map location	North latitude	West longitude	Depth (*metres*)	Type of station (work done)
540	South of Lona Bay	64° 17′	77° 39′	60	Plankton
541	5 miles west of Schooner Harbour	64° 25′	78° 05′	65–74	Plankton
542	Schooner Harbour	64° 24′	77° 56′	0–38	Plankton, benthos, littoral, hand line and long line fishing
543	Hydrographic section from Schooner Harbour to Southampton Island	64° 15′	78° 31′	265	Hydrographic
544		64° 07′	79° 05′	256	Plankton, hydrographic
545		63° 57′	79° 37′	338	Hydrographic
546	South of Seahorse Point	63° 44′	80° 13′	13	Plankton, hand line fishing
547	Near 546	63° 41′	80° 12′	73	Benthos (dredging)
548	Northernmost of islands off Seahorse Point	63° 47′	80° 08′	—	Walrus hunting
549	Evans Strait	63° 36′	82° 00′	73–75	Plankton, benthos (dredging), hydrographic
550	Evans Strait	63° 37′	82° 18′	—	Walrus hunting
551	Chesterfield Harbour entrance	63° 19′	90° 32′	90–110	Plankton, hydrographic
552	Chesterfield anchorage	63° 19.5′	90° 42′	18–25	Plankton, benthos (trawling)
553	Off Term Point	62° 09′	92° 25′	36–73	Plankton, benthos (trawling), hydrographic
554	30 miles south of Tavani	61° 28′	93° 07′	82	Plankton
555	North shore of Churchill	58° 47′	94° 10′	0	Littoral
1954					
601	West of Churchill River mouth	58° 50′	94° 17′	15	Productivity
602	Mouth of bay 7 miles south of Cape Pembroke, N.E. Coats Island	62° 51.5′	81° 54′	20	Plankton, productivity
603	Northeast of Coats Island	62° 55.5′	81° 41′	108	Plankton, benthos (dredging), hydrographic
604	13 miles northwest of Cape Pembroke	63° 08.5′	82° 05′	192	Plankton
605	Near 602	62° 51.2′	81° 54′	40	Plankton
606	3 miles southeast of Cape Pembroke	62° 55′	81° 48.5′	99	Plankton
607	South of Coats Island	62° 13′	83° 24′	14	Benthos (dredging)

Station	Map location	North latitude	West longitude	Depth (*metres*)	Type of station (work done)
608	West of Coats Island	62° 44.5′	83° 39′	32	Benthos (dredging)
609	Between Bencas and Coats Islands	62° 57.5′	82° 43′	18	Benthos (dredging)
610	Near 609	62° 58.5′	82° 41′	36	Benthos (dredging)
611	Near 610	62° 59.7′	82° 39′	49	Benthos (dredging)
612	Near 604	63° 06′	82° 08′	225	Plankton, benthos (dredging), hydrographic
613	2 miles north-east of Cape Pembroke	62° 57.2′	81° 50′	198	Plankton, benthos (dredging and trawling)
614	1 mile south-east of Cape Pembroke	62° 56′	81° 53′	13–18	Benthos (dredging)
615	Walrus Island	63° 15.5′	83° 43′	18–36	Benthos (dredging)
616	Walrus Island	63° 15.5′	83° 41′	85–90	Benthos (dredging)
617	Sugluk	62° 11.5′	75° 45′	100	Plankton, hydrographic
618	12 miles west of Burwell, Ungava Bay	60° 35′	65° 18′	329	Plankton, hydrographic
619	Near 514	62° 54′	81° 54′	0	Littoral
620	3 miles south-east of Cape Dorset	64° 12′	76° 27.5′	—	Plankton
621	South of Chorkbak Inlet	64° 17′	74° 38′	0	Littoral
622 & 534	Cape Dorset settlement	64° 14′	76° 33′	0–30	Benthos, long line fishing
623	South of Shugba Bay	64° 32.5′	74° 14′	—	Plankton
624	South of Keltie Inlet	64° 14′	73° 44′	0	Littoral
625	North of Alareak Island	64° 20′	75° 34.5′	0	Littoral
626	Chorbak Inlet	64° 38′	74° 33.5′	—	Plankton
627	North of Chorkbak Inlet	64° 43.5′	74° 50′	—	Plankton
628	Near 627	64° 46′	74° 55′	9	Hydrographic
629	Near 627	64° 47′	75° 02′	6.5	Plankton, hydrographic
630	Near 627	64° 52′	75° 04′	8	Plankton, hydrographic
631	Near 627	64° 47′	74° 58′	—	Fishing
632	Pudla Inlet	64° 21′	76° 12′	—	Littoral, benthos
633	Hobart Island	64° 12.5′	73° 14.5′	—	Benthos
634	9 miles north of Churchill	58° 54′	94° 10′	26	Hydrographic



Map showing positions of *Calanus* stations, 1953–54.

Frozen Oysters[1]

BY MARGARET L. MORTON[2] AND W. J. DYER[3]

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ABSTRACT

Quick frozen freshly shucked oysters stored at −10°F. (−23°C.) did not deteriorate significantly during a storage period of 9 months, as assessed by taste panels on the simmered oysters. Slow freezing and storage at higher temperatures resulted in a much greater loss in quality, and objectionable darkening occurred. Preparation as a stew largely masked this deterioration.

INTRODUCTION

BECAUSE of seasonal restrictions, a continuous supply of fresh Canadian Atlantic Coast oysters is not available. In addition the industry has a surplus of poorly shaped oysters which, although perfectly palatable, have to be graded low. If these could be marketed as frozen shucked oysters, a good market would be provided for this part of the supply. If they could be stored for 6 months to a year, then a continuous market supply would be available.

Pottinger *et al.* (1947) and Pottinger (1951) have stored frozen shucked oysters successfully for 6 months to a year at 0°F. (−18°C.). Packing in moisture-vapour-proof cellophane bags inside pint-size cartons was recommended. These authors stress that prevention of drying out during storage is essential and that only fresh oysters be used. No data were available in the literature on the effect of freezing rate or storage temperature. Since good freezing and cold storage facilities may not be readily available in the oyster-producing areas, it was deemed necessary to determine the effect of these factors. Norton *et al.* (1952) have shown that monosodium glutamate has some lengthening effect on storage time in various frozen foods in addition to its well known influence on taste. Accordingly, this additive was tested in our experiments on oysters.

EXPERIMENTAL

Fourteen gallons of freshly shucked oysters, *Ostrea virginica*, from the Bras d'Or Lakes, Nova Scotia, were brought to the laboratory by truck. They were washed in a 0.75% salt solution as recommended by Pottinger (1951) and drained. Monosodium glutamate was added to one lot of 3 gallons (13.6 l.) to a concentration of 0.1%. To prevent drying during storage, the oysters were packed in 8-oz. (225-g.) flat cans, then sealed and frozen. Half the untreated lot was slowly frozen,

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[2]Formerly of the staff of this station.

[3]This work was initiated at the request of the Atlantic Biological Station, St. Andrews, N.B.

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during about 15 hours, in moving air at 10°F. (—12°C.); the remainder, including the glutamate-treated lot, was quick frozen in brine at —10°F. (—23°C.). Half of each frozen lot was stored in constant temperature boxes at 10°F. and the other half at —10°F.

Analyses of crude fat, and pH and some moisture and protein determinations were carried out by methods described previously (Dyer and Morton, 1956).

Several preliminary tests were performed to determine the best way of preparing the samples for taste panel tests. Stewing, simmering, baking, and frying in deep fat were tried. It was found that all except simmering masked the flavour and texture, or gave difficulty in uniformity of preparation. The simmered samples were least palatable but differences in texture and taste could be readily distinguished. On this basis it was decided to simmer and stew the oyster samples for alternate taste panels. Samples were taken every 3 weeks and examined for colour, appearance, and odour.

For simmering, the frozen samples were placed in litre beakers just covered with hot water, and cooked until the edges of the oysters curled. The stew was prepared as follows: one 8-oz. can of the frozen oysters was heated with 50 ml. hot water and cooked as above; they were then added to 1 quart (1.1 l.) of hot milk; 2 tablespoons (50 g.) of butter, 1 teaspoon (5 g.) of salt and ½ teaspoon (2 g.) of pepper were added. The oysters were then served to a panel of four tasters, and were judged for texture, taste, and odour, using a scale of 0 to 5 for each. The grade given was converted to percentage for ease of calculation as used in previous taste panel work (Dyer and Dyer, 1949).

RESULTS AND DISCUSSION

Analyses

The average moisture content found was 90%. The total nitrogen was 0.83% and non-protein nitrogen 0.08%. The fat content averaged 2.7%, individual samples varying from 1.6 to 3.5%. The pH varied from 5.5 to 5.8 and showed no change on storage.

Appearance

A slight darkening appeared in 2 to 3 months in all the samples and this darkening intensified on storage up to 9 months. However, only the slowly frozen oysters stored at 10°F. (—12°C.) became badly discolored, which occurred after 6 months' storage. The reaction proceeded much further when the oysters were slowly frozen and stored at high temperatures. These conditions should therefore be avoided. This darkening was also noted by Pottinger (1951), who found that ascorbic acid did not prevent it. In our experiments glutamate similarly was of no benefit.

Taste Tests

Simmered Oysters

The average grades found by the taste panel are shown in Fig. 1. The quick frozen samples stored at —10°F. (—23°C.) showed only a slow drop in quality

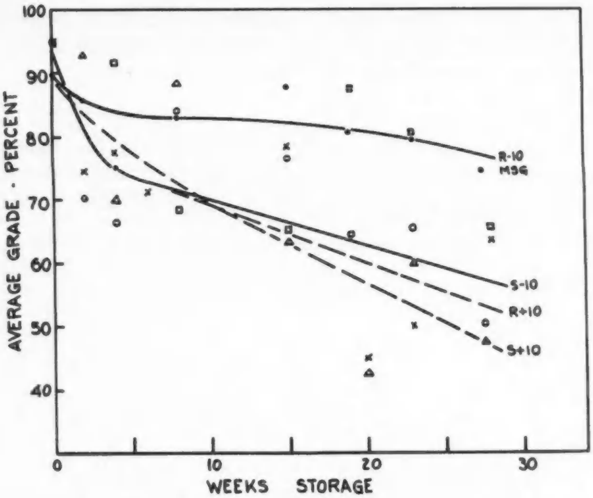

FIG. 1.—Average taste panel assessment of simmered oysters: Effect of freezing rate and storage temperature.

●	R—10	Rapid frozen, stored at —10°F. (—23°C.),
O	S—10	Slow frozen, stored at —10°F.,
×	R+10	Rapid frozen, stored at +10°F. (—12°C.),
Δ	S+10	Slow frozen, stored at +10°F.,
□	MSG	R—10 plus monosodium glutamate.

on storage up to at least 8 months, declining from an average grade of about 90% to about 80%. The monosodium glutamate-treated sample stored at the same temperature was mostly indistinguishable from the untreated one.

The samples stored at 10°F. (—12°C.) decreased in quality very much faster. The initial decrease was greater, to about 75% upon a month's storage, followed by a decline to 50 to 60% at 6 to 7 months. The slowly frozen sample stored at —10°F. was only slightly better.

The curves for texture and taste are not plotted separately since they were similar to those for the average grade. The texture in the case of the quick frozen sample was slightly better than the average grade, and slightly poorer in the other samples. The taste judgments were very similar to the average.

Thus the taste panels conducted on the simmered samples show a rapid deterioration in quality in both texture and taste for all the samples except the quick frozen one stored at —10°F. As found with frozen fish (Dyer, 1951) a low storage temperature, —10°F. or less, is necessary to inhibit deterioration on storage, and in the case of oysters rapid freezing seems also to be essential.

It should be remembered that these experiments were conducted in almost full sealed cans and desiccation did not occur during storage. If moisture-proof bags of cellophane or similar material were used industrially, then care would

have to be taken to leave only a small air space in the top of the sealed bag and to use a carton or overwrap to avoid punctures, as Pottinger (1951) points out. Again a low storage temperature would retard the desiccation.

Stewed Oysters

Served in this manner the oysters were delicious. No change could be detected throughout the storage period, nor was there any difference resulting from the various treatments (Fig. 2). Apparently the changes occurring were

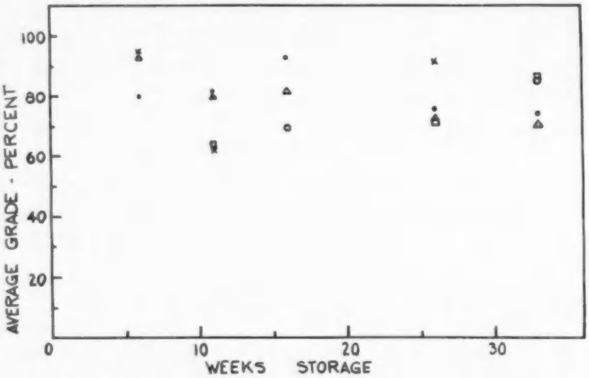

FIG. 2.—Average taste panel assessment of stewed oysters: Effect of freezing rate and storage temperature. (Points as in Fig. 1.)

completely masked by this method of preparation. This seems to be the case also with deep frying, as Pottinger *et al.* (1947) found little or no change on storage using this cooking method. Thus, while deterioration does occur during frozen storage, especially following slow freezing and at insufficiently low storage temperatures, in practice it seems that this deterioration in quality can be masked if the oysters are served stewed or deep fried. Of course this does not apply to the appearance of the oysters before preparation, and they could not be served on the half shell.

SUMMARY

Experiments on the storage of frozen shucked oysters have shown that deterioration occurs in frozen storage if they are slowly frozen and when stored at 10°F. (−12°C.). Little change in texture or taste occurs with quick frozen samples stored at −10°F. (−23°C.) when desiccation is held to a minimum. Even these changes can be masked when the oysters are served as a stew or deep fried. However if drying out occurred, the masking might not be as complete. Considerable darkening does take place on storage, especially under the poorer conditions.

It is concluded that fresh oysters properly frozen and stored can be kept frozen satisfactorily for at least 9 months, thus providing a practical off-season

supply, and a market for mis-shapen oysters which cannot be satisfactorily marketed for consumption in the fresh oyster trade.

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The Net Plankton of Great Slave Lake[1]

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CONTENTS

ABSTRACT

The net plankton of Great Slave Lake was studied extensively in the years 1944 to 1947 and sampling continued at a central station through 1954. Some 490 samples were taken using large nets and traps with No. 20 silk. Taxonomic, gravimetric and numerical analyses are reported and comparisons made between the larger, open lake and the deep, cold, east arm.

Among 160 species of algae, two diatoms, *Melosira islandica* and *Asterionella formosa* were dominant. Green and blue-green algae were scanty but *Dinobryon* was numerous, especially in the cold, east arm. Among 26 rotifers *Keratella cochlearis* and *Kellicottia longispina* were dominant and four other species common. Cladocera were scarce but the copepods made up about 85% of the plankton volume. *Diaptomus* spp., *Cyclops* spp., *Limnocalanus macrurus*, *Epischura lacustris* and *Senecella calanoides* were the main species.

The average dry weight of the standing crop of net plankton in the open water was 21.8 kg./ha. The crop was heavier in years of warm water than in those of colder water. Occasional high turbidity was associated with decreased plankton. In Christie and McLeod Bays of the east arm, where the waters are deeper, colder and lower in mineral content, the

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average dry weight of plankton was 14.3 and 9.0 kg./ha. These amounts are typical of the plankton in large, very oligotrophic lakes.

An early season maximum of diatoms and copepods was followed by a rapid decline in late July. The smaller, late-summer maximum included large numbers of rotifers. More than half of the plankton was in the upper 25 metres with decreasing amounts down to 100 metres. A thin plankton, mainly of copepods, extends down to 600 metres.

The dominant species of plankters in the open water of Great Slave Lake appear to be almost identical with those of Lake Winnipeg, Lake Nipigon and the Great Lakes. All have a diatom-copepod type of plankton with a constant group of rotifers and *Dinobryon* in moderate numbers. Green and blue-green algae are scanty except in the shallower and warmer lakes, Winnipeg and Erie.

INTRODUCTION

This study was part of the general investigation of the biology and fisheries of Great Slave Lake begun by the writer and several associates in May, 1944. Our purpose was to investigate the productivity and, if possible, to predict the fishery from this large lake. Since plankton is the primary producer of organic matter in the lake, its importance in fish production is self-evident. Thus, on theoretical grounds, perhaps we should have begun with an intensive study of the plankton. In practice however, it is well known that plankton production is extremely difficult to measure or estimate, especially in such large and varied areas as those which make up Great Slave Lake. Our decision, therefore, was to follow a middle course, devoting a moderate proportion of the time available for field operations to the sampling of plankton. The program included an exploration of the plankton in all parts of the lake. Quantitative samples were taken throughout each summer season to arrive at an estimate of the standing crop of net plankton. More intensive and longer continued sampling was carried on at a few locations to follow seasonal changes and, if possible, to correlate these with observed physical and chemical conditions. It seemed evident however, that the main aim should be a description of the plankton population and the provision of suitable quantitative data for comparison of the plankton of Great Slave with that of other lakes.

MATERIALS AND METHODS

Extent and Distribution of Sampling

In the summers 1944 to 1947 plankton was collected at 57 numbered stations and in a few inshore localities to which no numbers were assigned. Collections at a single station (No. 31, off Gros Cap) have been continued from 1946 to 1954. Thus we have some data on the plankton of Great Slave Lake over a total period of 11 years. In the first two seasons, 1944 and 1945, it was necessary to explore most of the lake's area. Thus stations set up in these years were rarely visited more than twice per summer. In 1946 and 1947, with the reconnaissance completed and two boats in operation, it was possible to have sampling at several stations repeated throughout the summer. The aim was to repeat these at approximately weekly intervals. From 1948 to 1954 collection at Station 31 has been continued through the cooperation of Dr. W. A. Kennedy and his staff engaged in sampling the fish harvest from the lake. In these years an attempt was made

to take samples at 10-day intervals. In the 10 years of sampling collections have been made on 154 occasions. This includes repeated samples at numerous stations. The collections made at any station on any one day were never less than three and often much more than this when vertical series were taken. Thus the study is based on the examination of some 490 samples.

The locations of most of the numbered sampling stations are indicated in the maps, Fig. 1, 2 and 3. The stations are listed in Table I which indicates also their

TABLE I. Stations for plankton collection in Great Slave Lake.

Station number	Location	General area	Depth
			metres
1	1 mi. W. of Round Is.	Main	11
2	1 mi. S.E. of Egg Is.	Main	30
3	25 mi. NW. of Resolution	Main	44
4	10 mi. E. of Gypsum Pt.	North Arm	95
5	10 mi. S. of Yellowknife	North Arm	63
6	Mouth of Frank Chan. near Rae	North Arm	2
7	1 mi. S. of Yellowknife	North Arm	12
8	8 mi. NE. of Redrock Pt.	North Arm	35
9	8 mi. S. of West Mirage Is.	North Arm	30
10	6 mi. NW. of Outpost Is.	Main	65
11	30 mi. E. of Jones Pt.	Main	58
12	2 mi. E. of Sachowia Pt.	Islands	185
13	6 mi. NW. of Sentinel Pt.	McLeod Bay	185
14	1 mi. W. of Snowdrift	Christie Bay	28
15	10 mi. E. of Old Fort Is.	North Arm	8
16	0.2 mi. E. of Joliffe Is., Yellowknife	North Arm	13
17	0.5 mi. S. of Round Is.	Main	7
18	3 mi. NE. of mine at Outpost Is.	Islands	97
19	E. end of mine chan., Outpost Is.	Islands	11
20	W. end of mine chan., Outpost Is.	Islands	3
21	0.5 mi. N. of Outpost Is.	Islands	23
22	0.5 mi. W. of Outpost Is.	Islands	36
23	South of inner bay, Yellowknife	North Arm	1
24	Centre of inner bay, Yellowknife	North Arm	3
25	6 mi. W. of Outpost Is.	Main	60
26	6 mi. NNW. of Grant Pt.	Islands	15
27	11 mi. N. of Slave Delta	Main	68
28	5 mi. SE. of Bigstone Pt.	McLeod Bay	280
29	5 mi. S. of Hoarfrost R.	McLeod Bay	72
30	5 mi. NW. of Redcliffe Is.	Christie Bay	340
31	1.5 mi. SW. of Gros Cap	Main	140
32	10 mi. WW. of Egg. Is.	Main	23
33	12 mi. N. of Slave Delta	Main	90
34	25 mi. E. of Jones Pt.	Main	66
35	1 mi. S. of Pearson Harbour	Christie Bay	140
36	4 mi. N. of Pearson Harbour	Christie Bay	600
37	1 mi. SW. of Iron Is.	Islands	68
38	10 mi. SW. of Whaleback Is.	Main	105
39	1.5 mi. NW. of W. end, Union Is.	Islands	150
40	Centre of Inconnu Chan.	Islands	40
41	Near outlet, Stark Lake, Snowdrift	Christie Bay	60
42	Centre of Wildbread Bay	Christie Bay	116
43	East end Gros Cap Chan.	Main	16
44	Centre of Gros Cap Chan.	Main	7
45	10 mi. NEE. of Gibralter Pt.	McLeod Bay	150
46	N. entrance to Pearson Harbour	Christie Bay	12
47	3 mi. S. from W. end Caribou Is.	Islands	60
48	1 mi. S. from W. end Blanchet Is.	Islands	50
49	7 mi. N. of Hay River	Main	20
50	5 mi. SE. of Gros Cap	Islands	210
51	15 mi. W. of Matonabbee Pt.	North Arm	50
52	Off Lobstick Is.	North Arm	20
53	5 mi. SE. of East Mirage Is.	North Arm	20
54	10 mi. SE. of Hardisty Is.	Main	37
55	10 mi. S. of Whaleback Is.	Main	65
56	12 mi. SW. of Outpost Is.	Main	115
57	9 mi. NW. of Slave Delta	Main	99

approximate position and the depth of water. The choice of these locations was dictated largely by the plan for exploring the major areas of the lake. Thus about 20 stations were in the main or open part of the lake, 13 in the north arm (of these 5 were in Yellowknife Bay), 13 in the Islands area, 7 in Christie Bay and 4 in McLeod Bay. The few stations chosen for seasonally repeated sampling were considered representative of important parts of the lake. The longest series of samples is at Station 31, off Gros Cap and close to the geographic centre of the lake. This, of course, does not guarantee that it can be considered as representative of the main lake, a question which will be considered later. It should be noted that the stations listed here for plankton sampling are those at which physical and chemical observations were made. Much of this physical and chemical data has been presented in an earlier paper (Rawson, 1950) to which frequent reference will be made in this report.

At each station and at each time of sampling, a minimum of three samples was taken. This included two total vertical hauls with the large net (described below) and either a 3-minute surface tow or a 50-litre surface sample. The

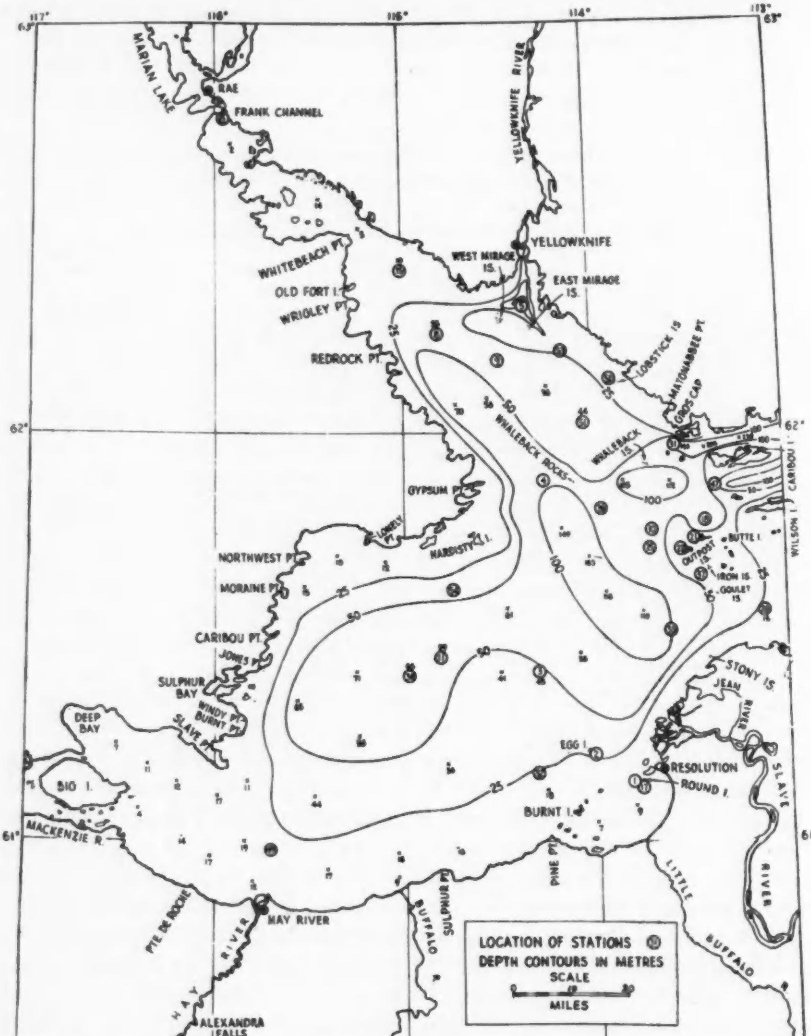

Fig. 1.—Map of the main part of Great Slave Lake showing depth contours and location of stations for plankton collection.

duplication of total vertical hauls allowed the use of one for determination of dry weight and organic matter while the other remained for species determination and numerical analysis. The surface samples were primarily for qualitative

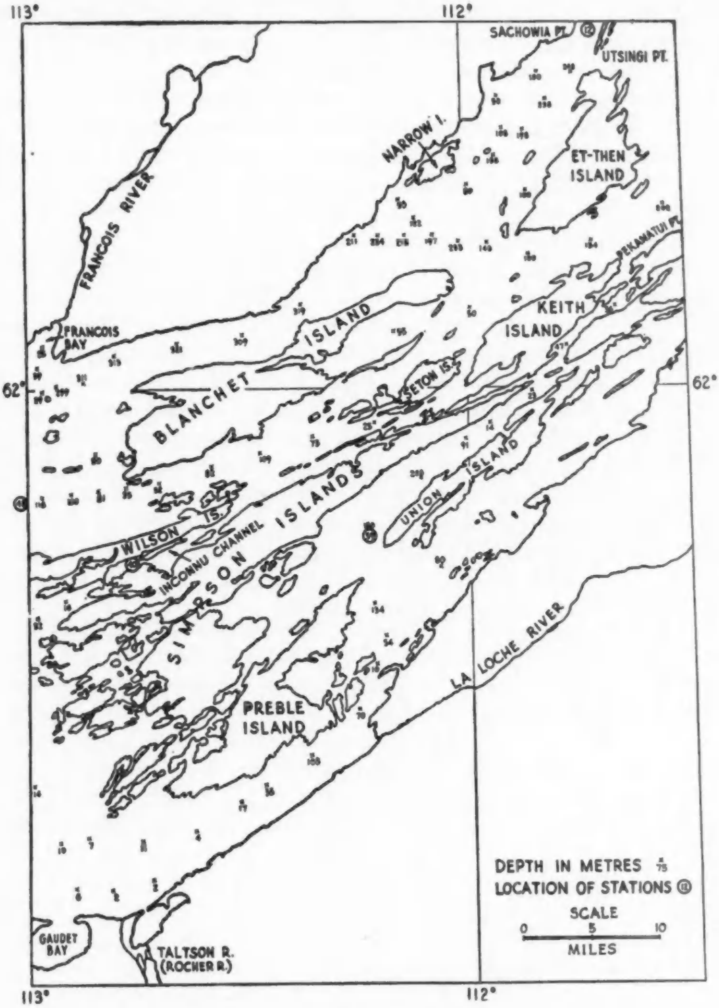

FIG. 2.—Map of the "Islands Section" of Great Slave Lake.

examination but their analysis has revealed certain features not evident from our other quantitative samples.

The use of total vertical hauls as representative of the plankton in a given area was intended to cope with the known irregularities in vertical distribution including those caused by diurnal migration. The possibility of horizontal irregularities in distribution was not overlooked for, as Baldi *et al.* (1945) have shown, even in a fairly large oligotrophic lake (Lake Maggiore), significant differences

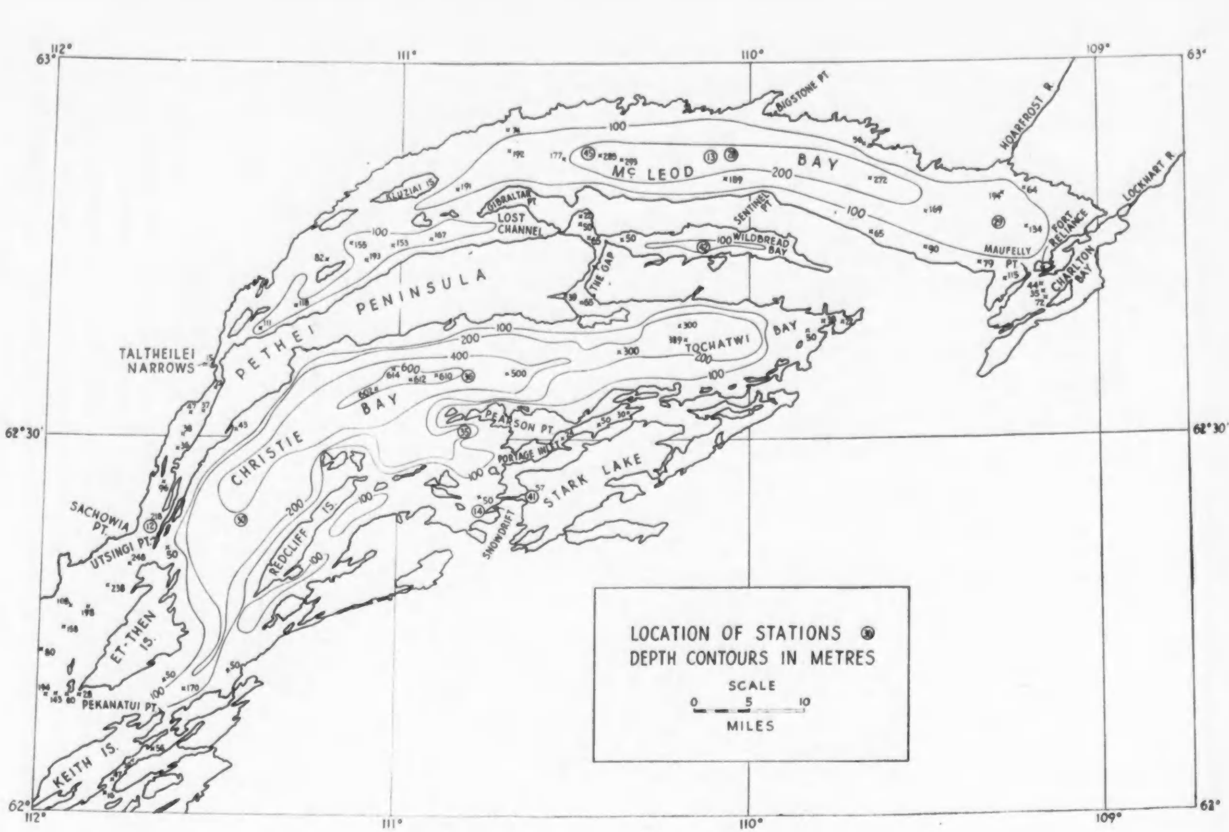

FIG. 3.—Map of the east arm of Great Slave Lake.

may occur between the plankton at nearby stations. Nevertheless, it was felt that, because of the limited time available, little could be done in the way of increasing the number of sampling stations. The good agreement between the plankton at Station 31 and that of several stations in the open lake, and the absence of any gross irregularities in the quantitative data presented below, give some encouragement for the belief that, in the open water areas of Great Slave Lake, horizontal irregularities in plankton distribution are not extensive.

In addition to the total vertical hauls, there were taken at various stations and times, fractional vertical hauls to determine depth distribution of plankton. These were taken both with the standard type of closing net and with the Clarke-Bumpus sampler, hitched so that it could be used vertically. Additional plankton sampling included hauls for the calibration of nets against the Clarke-Bumpus sampler and against samples taken with the 10-litre sampler described below. Interesting collections of Entomostraca were taken occasionally in the coarse-mesh nets designed for the capture of *Mysis* in studies made by Larkin (1948).

Most of the sampling effort was concentrated on the plankton of the open water on the assumption that this large area is most important in the productivity cycle. However, the rich and varied inshore plankton population was not ignored and from time to time tows were made in the shallow protected regions. These were entirely qualitative and were taken because of their interest to those studying the geographic distribution of plankton organisms.

Equipment and Techniques of Sampling

The techniques used in the present study are those adopted and standardized by the author over a period of some 25 years in lakes of Western Canada. Some of the results of these studies and a criticism of the methods used were published in a recent paper in this journal (Rawson, 1953b).

The large net which the writer has used in this and other investigations has a mouth of diameter 25 cm., opening into a truncated cone of heavy close-woven cotton 30 cm. long leading to a centre ring 30 cm. in diameter. The straining cone is 60 cm. long and carries the usual straining bucket, 12 cm. long and 5 cm. in diameter, attached to a collar on the lower end of the net by means of a bayonet fitting. The straining cone is of No. 20 silk bolting cloth with 68 meshes per centimetre (173 per inch). The average diameter of the apertures in several samples of bolting cloth was approximately 50 microns. The suspension of the net was such that it could also be used as a closing net for vertical series. This net was adopted because in vertical hauls it took sufficient quantities of plankton for convenient determinations of dry weight and ash content and also because it takes, with moderate efficiency, most zooplankters and a large fraction of the phytoplankton species. Its handicaps lie mainly in the difficulty of determining and maintaining its efficiency. In many investigations it might be preferable to use a coarser (and more efficient) silk for the zooplankters and a settling or centrifuging method to collect the phytoplankton. The time available for plankton sampling in the Great Slave study did not allow these refinements.

In making total vertical hauls with the large net, it was attached to a line in such a way that a sounding iron hung about 0.5 metre below the bucket. The net was lowered until the sounding iron just touched bottom, then hauled to the surface at the rate of 0.5 metre per second. Various precautions were taken to maintain the efficiency of these nets. Several new nets were provided at the beginning of each season and the silk on the bucket (which tends to become clogged before the remainder of the net) was replaced usually three times during the season. The net was washed vigorously immediately after each haul. Surface tows, which often encounter dense algal populations and thus clog the nets rapidly, were not taken with the nets used for vertical hauls. With such treatment the nets used in Great Slave Lake showed an efficiency of 38 to 45% at the beginning of the season and 24 to 29.5% at the end. It should be noted that in other situations, especially in eutrophic lakes where blue-green algae are frequent, we have found more rapid deterioration in efficiency despite the precautions described above.

Net calibrations were made in a variety of ways, comparing the catch from a vertical haul through a known column with that obtained by trap samples or the Clarke-Bumpus sampler through an identical column. The Clarke-Bumpus sampler gave fairly consistent results but from our own and other investigators' results, there is some doubt as to the accuracy of the flow recording mechanism when the sampler is used at moderate rates of haul and with a fine-mesh (No. 20) net. A 10-litre Juday trap was used in the early part of the investigation but found to be slow and awkward to handle and subject to considerable error by leakage while the water was draining through the small strainer. Thus a new type of 10-litre trap was constructed as described below. This trap was a cylinder, 0.5 metre in length and closing at both ends with damper-type valves. Ten-litre samples were taken at 0.5-metre intervals through the upper 10 metres. These were hauled to the surface and strained by releasing them into the large plankton net. In this way the catch from a complete column of water could be compared with the catch from a plankton net hauled at 0.5 metre per second through a similar column. Comparison of the two catches could be made by counting suitable organisms but were found to be made more conveniently by determining the dry weight of the comparable samples. Calibrations were usually made for each net at the beginning, in the middle and at the end of the season's activities. Since the decline in efficiency was fairly uniform it would be possible to estimate the efficiency at any date. However the total range of variation in efficiency of the nets used in Great Slave Lake is not excessive, so the average rate of efficiency of 37% has been used throughout in calculating population figures from sampling measurements. Since the area of the mouth of the plankton net was 490 sq. cm. and the average efficiency 37%, the amounts listed in various tables per total vertical haul, can be converted to amounts per square metre by multiplying by 55.

In using the trap for calibration it was found that twenty samples taken at 0.5-metre intervals in the upper 10 metres invariably took less than twice as much plankton as ten samples at 1-metre intervals. The discrepancy was com-

monly as great as 10 or 15%. A somewhat comparable discrepancy has been noted by many workers, e.g. Ricker (1938), between the sum of stage hauls and the total vertical catch with a closing net. This has been attributed frequently to spilling when the net is closed and this may well be involved but with our 0.5-metre trap such losses could not occur. It seems probable that the disturbance of taking 20 samples in one spot may have driven away some of the Entomostraca. Partial verification of this theory was obtained by moving the boat a short distance between each sampling. When this was done the plankton from 20 samples was close to double that from 10 samples. In this connection we may note that Lindstrom (1952) found it desirable to move his boat in a 12-metre circle while sampling zooplankters in Swedish lakes.

The new plankton trap is illustrated by the photograph and the diagram of its closing mechanism, in Fig. 4. The tube was made up of heavy galvanized iron 16 cm. inside diameter and of sufficient length that the closing valves could be 50 cm. apart. The remainder of the mechanism is of brass. The essentials are two disc-shaped valves which are vertical in the open position and which close by rotation to come into contact with narrow, semicircular shoulders. The shoulders at the lower end of the sampler are provided with a soft rubber gasket although the first model, made without this feature, did not show excessive leakage. Closure of the sampler is accomplished by means of a messenger which releases the bar *A*, which pulls directly on the upper valve, and the latter is linked to the lower valve by means of the slender rod inside the sampler. Thus the valves are held tightly closed as long as the weight of the sampler and its contents are supported by the cable on which it is operated. The drawing, Fig. 4, shows the principle, but not the details of construction of the sampler. The author would be pleased to provide, at cost, a 1/2-scale blueprint of the sampler to anyone wishing this information.

Previous cylindrical samplers of large capacity have been described by Strøm (1931), Rodhe (1941) and Lindstrom (1952). These have wide-open ends which are closed by heavy trap-doors hinged at one side. This necessitates the use of heavy levers and external springs for closing. Our new sampler is lighter and has no springs or lateral projections. For our purposes also, additional advantages were the large sample (10 litres and 0.5 metre in length) and the rapid straining achieved by emptying the contents through a large plankton net.

Surface samples of plankton in our previous work had been taken by towing a net with the upper edge of the mouth just breaking the water surface for a period of 3 minutes at "rowing speed". It was realized that towing rate and net efficiency varied greatly in this procedure and as a result the samples were not used for quantitative purposes. Some tests of the efficiency of these tows were made by towing the regular net parallel to the Clarke-Bumpus sampler. The results were so variable that it was decided to change to a simpler and much more accurate method of sampling the surface plankton. The procedure used in the latter part of the Slave Lake investigation and in more recent work, has been to dip up 50 litres of water from the upper 20 cm. of the lake and to pour it into a large plankton net. The dipping was done with a standard metal gallon measure

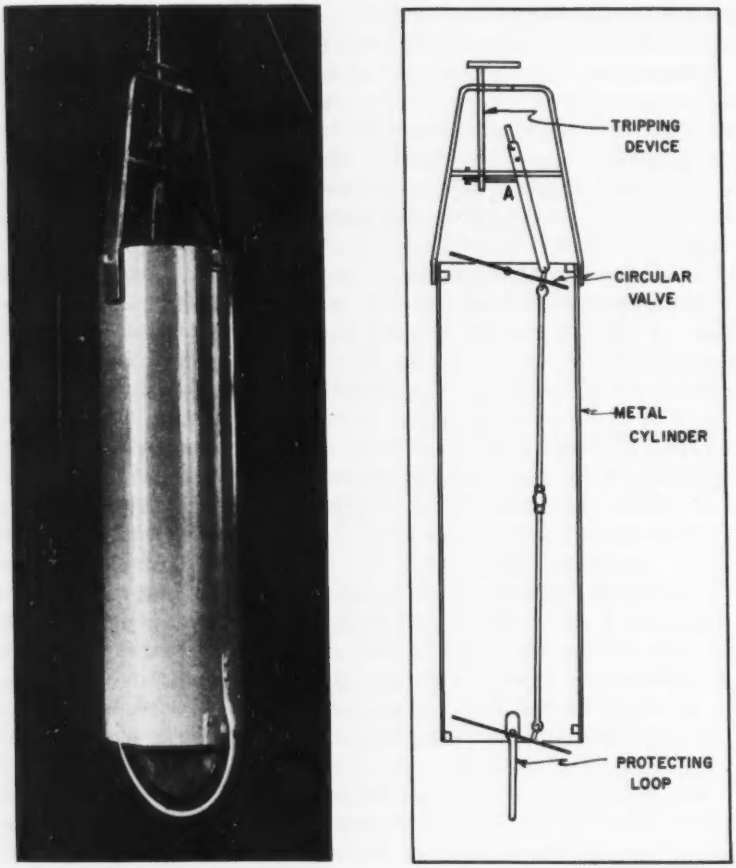

FIG. 4.—Left: the 10-litre cylindrical plankton trap shown open. Right: diagram of the mechanism.

(11 imperial gallons = 50 litres). These measures are inexpensive and widely available.

Preservation of the plankton samples was accomplished by adding formalin to the amount of 5% (1/20 of the volume) of the sample of plankton in lake water. This method of preservation has been satisfactory for general purposes although some taxonomists prefer other treatment for particular groups of organisms. It was found also that in making gravimetric analysis of very small samples (less than 100 mg. dry weight) a correction for the residue from formalin and lake water should be made. This was done either by drying an equivalent volume of the preserving solution or by washing the sample in distilled water. In a few instances samples were preserved in 70% ethyl alcohol. This was less convenient than formalin, both in the field and later, for handling in the laboratory.

Laboratory Analyses

All samples were examined microscopically to determine the genera and species represented. Organisms were listed as A for abundant, C for common, O for occasional or R for rare, in each collection. These data provided a general picture of the plankton and a basis on which suitable samples were selected for submission to specialists in the various taxonomic groups. The identity of all common species was verified before counting operations were begun. Acknowledgement of the very generous help of a number of systematists is made in the appropriate sections below.

Gravimetric determinations were made by drying the plankton samples in porcelain crucibles in an oven at 60°C. for 48 hours or until a constant weight was reached. Weighing was done on a chemical balance sensitive to 0.1 mg. The sample was then ashed over a bunsen burner taking care that ignition was slow so that no ash particles were carried away. The loss on ignition was assumed to be equivalent to the organic matter in the original sample. It was also assumed that this organic material was generally autochthonous (planktonic) in origin although in a few samples significant quantities of wood fibres were observed. In discussing the quantity of the standing crop of plankton, the dry weight in kilograms per hectare is used. However the amount and percentage of organic matter in each sample is recorded in Tables II and III below, so the data may be expressed in terms of organic matter if that is desired.

Numerical analysis has included separate counts of zooplankters and phytoplankters. The former were counted in cells of 1 or 3 ml. capacity using a mechanical stage on a binocular microscope. When necessary the sample was fractioned using a 1-ml. Stempel pipette but in some instances it was possible to count the whole sample. Occasionally the Entomostraca were counted in the whole sample but the rotifers only in a small fraction.

Phytoplankters were counted in the usual Sedgwick-Rafter cell, 1 ml. in capacity and $20 \times 50 \times 1$ mm. in dimensions. After adjusting the original sample to an appropriate volume, a 1-ml. sample was transferred with the Stempel pipette to the counting cell and a cover slip applied. Counting was usually done with $10\times$ oculars, one of which was supplied with a squared-field disc, and a $13\times$ objective. The latter had a long working distance which was convenient for work in counting cells. Counts were made of at least 15 fields and as many more as was necessary to obtain satisfactory counts of all but the rarer organisms. It was found convenient to count the filamentous and colonial phytoplankters in arbitrary units listed as follows: *Anabaena* 10 cells, *Asterionella* 8, *Dictyosphaerium* 25, *Dinobryon* 10, *Fragilaria* 10, *Melosira* 5, *Pediastrum* 25, *Tabellaria* 5. However, these units were converted to cell numbers for the tables in this paper.

Calculation of volume equivalents for phyto- and zooplankters was made by the method of Lohman (1908) and with the help of factors recorded by Fair and Whipple (1927). These equivalents make possible the calculation of volumetric, as distinguished from numerical, dominance of the organisms occurring in the hauls, also the $p{:}z$ ratio, i.e. the ratio of total volume of phytoplankters to

zooplankters. While p:z ratio in *total* plankton is of great interest, it is felt that such data for net plankton is of somewhat limited significance. For this reason the determination of p:z ratios has been carried out only on yearly averages for Station 31 and on certain samples selected as representative of different areas and seasons.

In view of the uneven vertical distribution of plankton and the further complication of extensive diurnal migrations of many zooplankters, it seemed that the best method of recording the plankton crop in numbers or weight would be per unit area. This has been done in this study by recording numbers per "total vertical haul" and weight in kilograms per hectare. Numbers per vertical haul with our nets can be converted to numbers per square metre by multiplying by a factor of 55. Expressing the amounts of a plankton crop per unit area, although less misleading than numbers per unit volume, still has some limitations. A total vertical sample at a shallow station is smaller and not directly comparable to a sample from a deeper station. This situation is more troublesome in a deep oligotrophic lake, such as Great Slave, where the thin plankton penetrates to a great depth, than in a shallow eutrophic lake where the bulk of the plankton is confined to the upper layers.

SPECIES COMPOSITION OF THE NET PLANKTON

A careful determination of the species present is prerequisite to an ecological consideration of the plankton and, while determination of the more abundant forms would have served most of our purposes, a more complete study is of interest in problems of geographic distribution. Our first concern was with the open water region, thus about 90% of the 490 samples are from this area while the remaining 10% were from shallow, inshore localities. While no special search was made for rare occurrences, it is felt that our list is reasonably complete for the open water species. It is probably quite incomplete for the rich and varied shallow water species.

The following lists are annotated to indicate what is known of the abundance and distribution of the various species in the several parts of the lake. In the later sections dealing with quantitative studies, only those species or genera which appear in considerable numbers in the limnetic plankton are considered.

The Phytoplankton

The algae have been identified by the Rev. P. Kuehne, of Annaheim, Saskatchewan. My profound thanks are due to him for his painstaking examination of more than one hundred collections during a period of several years. The classification followed is that proposed by Smith (1950). In the year 1945 a special effort was made to obtain collections from a wide variety of localities. Thus in addition to the regular samples at the many open water stations collections were made in shallow water at four main locations. These were Resolution, on the muddy south shore; the Outpost Islands, a rocky protected area in mid-lake; Gros Cap on the rocky precambrian shoreline and the inner bay

at Yellowknife, a protected harbour with relatively warm water. Since few inshore collections were made in other parts of the lake, most of the shallow-water species in the following text are recorded from one or more of these four localities. Of about 160 species and varieties listed only some 35 are primarily from the rich inshore environment which was still not extensively sampled.

Adjectives such as rare, frequent, etc. in the following list refer only to frequency in our samples. Further collecting might well demonstrate that forms we list as rare are abundant in other parts of the lake.

DIVISION CHLOROPHYTA

Chlorophyceae

Volvocaceae

Pandorina morum Bory. Taken in surface samples at many stations in and around the main lake. Usually in small numbers.

Eudorina elegans Ehr. Rare in main lake and in Christie Bay.

Volvox mononae G. M. Smith. Rare in a surface sample, Yellowknife Bay.

Palmellaceae

Sphaerocystis schroeteri Chod. Frequent in all parts of the lake, including McLeod and Christie Bays.

Tetrasporaceae

Tetraspora lubrica (Roth) Ag. Common in one haul at Outpost Island.

Ulotrichaceae

Ulothrix zonata (Web. and Mohr) Kütz. Inshore at Yellowknife and Outpost Island.

Chaetophoraceae

Chaetophora incrassata (Huds.) Hazen. Rare at Outpost Island.

Cladophoraceae

Cladophora spp. Fragments inshore at Gros Cap and Resolution.

Oedogoniaceae

Bulbochaete sp. Fragments inshore at Yellowknife and Outpost.

Characiaceae

Characium gracilipes Lambert. Rare inshore at Outpost Island.

Hydrodictyaceae

Pediastrum boryanum (Turp.) Menegh. Widespread in samples around main lake. Common at Gros Cap at Midsummer and later.

Pediastrum duplex Meyen. Rare, inshore at Outpost and Resolution.

Pediastrum duplex var. *clathratum* (A. Br.) Lagerh. Rare, in Islands area.

Pediastrum duplex var. *gracillimum* W. and G. S. West. Only at Outpost Island.

Pediastrum glanduliferum Benn. Rare at Outpost and near Slave Delta.

Pediastrum kawraiskyi Schmidle. Rare, taken only inshore at Resolution.

Pediastrum tetras (Ehr.) Ralfs. Rare, taken only at Outpost Island.

Sorastrum americanum (Bohlin) Schmidle. Rare at Outpost Island.

Oocystaceae

Ankistrodesmus falcatus (Corda) Ralfs. Occasional, inshore at Outpost Island.
Ankistrodesmus spiralis (Turner) Lemm. Rare near Outpost Island and in McLeod Bay.
Dictyosphaerium pulchellum Wood. Widespread in the main lake, common at Gros Cap in late season, rare in Christie Bay.
Oocystis borgei Snow. Rare, taken only in the north arm.
Selenastrum westii G. M. Smith. Rare, only inshore at Outpost Island.

Scenedesmaceae

Crucigenia quadrata Morren. Rare, only in north arm.
Crucigenia rectangularis (Näg.) Gay. Occasional inshore at Outpost Island.
Scenedesmus arcuatus Lemm. One collection only at Outpost Island.
Scenedesmus bijuga (Turp.) Lagerh. Common in shallow water in Islands area.

Zygnemataceae

Mougeotia sp. Rare inshore at Yellowknife and Resolution.
Spirogyra spp. Common in inshore samples from Yellowknife, Resolution and Outpost.
Zygnema spp. Common at Outpost and Yellowknife.

Mesotaeniaceae

Gonatozygon kihnahani (Arch.) Rabenh. Rare, Yellowknife Bay only.

Desmidiaceae

Closterium acerosum (Schrank) Ehr. Rare, inshore at Outpost.
Closterium aciculare T. West. Occasional, taken only in Yellowknife Bay.
Closterium cornu Ehr. Over deep water in mid-lake.
Closterium moniliferum (Bory) Ehr. Rare in shallows at Gros Cap and Outpost Island.
Cosmarium binum Nordst. Rare at Gros Cap and Outpost.
Cosmarium botrytis (Bory) Mengh. Common inshore around main lake.
Cosmarium circulare Reinsch. One collection at Outpost.
Cosmarium impressulum Elfo. Common inshore around main lake.
Cosmarium margaritatum (Lund) Roy and Biss. Common Outpost and Resolution.
Cosmarium punctulatum Bréb. Rare at Outpost and Resolution.
Cosmarium pyramidatum Bréb. Rare at Outpost.
Cosmarium rectangulare Grün. Rare at Outpost.
Cosmarium subcrenatum Hantzsch. Common at Outpost.
Cosmarium subcucumis Schmidle. Rare at Outpost.
Cosmarium turpinii Bréb. Common at Outpost.
Cosmarium spp. in Yellowknife Bay.
Hyalotheca dissiliens (Smith) Bréb. Rare, Yellowknife Bay only.
Hyalotheca mucosa (Dillw.) Ehr. Rare, Yellowknife Bay only.
Pleurotaenium trabecula (Ehr.) Naeg. Inshore only at Yellowknife.
Pleurotaenium truncatum (Bréb.) Naeg. Rare, inshore at Outpost.
Spondylosium planum (Wolle) W. and G. S. West. Occasional in McLeod Bay and Artillery Lake.
Staurastrum anatinum Cooke and Wills. Rare, in Christie Bay only.
Staurastrum anatinum var. *curtum* G. M. Smith. Outpost only.
Staurastrum bullardii G. M. Smith. Outpost only.
Staurastrum furcigerum var. *armigerum* (Bréb.) Nordst. Outpost only.
Staurastrum polymorphum Bréb. Several collections at Outpost Island.

DIVISION CHRYSOPHYTA

Xanthophyceae

Botryococcus braunii Kütz. Rare, taken only in McLeod Bay.
Characiopsis sp. Frequent in main lake and north arm.
Tribonema bombycinum (Ag.) Derb. and Sol. Rare, taken only in the north arm.

Chrysophyceae

Dinobryon divergens Imhof. Common and often abundant in all parts of the main lake. Rare in the East arm.
Dinobryon sertularia Ehr. Rare, taken only in Yellowknife Bay.
Dinobryon stipitatum Stein. Frequent in the main lake and common in McLeod and Christie Bays.
Mallomonas alpina Pasch. and Ruttner. Frequently taken in small numbers at Outpost and Yellowknife.

Baccilariophyceae

Coscinodiscaceae

Cyclotella comta (Ehr.) Kütz. Common inshore at the Slave Delta, Resolution and Outpost.
Cyclotella meneghiniana Kütz. Common at offshore stations in the main lake.
Cyclotella sp. Common at offshore stations.
Melosira arenaria Moore. Rare in two collections, Slave Delta and Outpost.
Melosira islandica O. Müll. One of the most abundant diatoms in Great Slave Lake. Taken in most of the samples and in all parts of the lake.
Melosira varians Ag. Occasional in samples from Outpost and Yellowknife Bay.
Stephanodiscus astraea (Ehr.) Grun.
Stephanodiscus niagarae Ehr. The two species af *Stephanodiscus* were common and widespread in the main lake, north arm, Christie and McLeod Bays. They are similar in general appearance and cannot be differentiated at magnifications used in our counting cells. Special clearing of a few samples suggests that they are about equally numerous.

Rhizosoleniaceae

Rhizosolenia eriensis H. L. Smith. Common and rarely abundant at Resolution, Yellowknife main lake and McLeod Bay but not observed in Christie Bay.

Tabellariaceae

Tabellaria fenestrata (Lyngb.) Kütz. Present in moderate numbers in nearly half of the samples taken. Found in all parts of the lake including McLeod and Christie Bays.
Tabellaria flocculosa (Roth) Kütz. Slightly less numerous than the previous species but equally widespread.
Diatoma elongatum Ag. Numerous in all parts of the lake except McLeod Bay.
Diatoma vulgare Bory. Rare, taken only in Yellowknife Bay and north arm.

Fragilariaceae

Asterionella formosa Has. Very common and widespread. Second only to *Melosira* in abundance.
Asterionella gracillima (Hentzsch) Heib. Rare at station near Jones Point.
Fragilaria capucina Desmaz. Common in all parts of the lake, except McLeod Bay.
Fragilaria crotonensis Kitton. Widespread but usually near shore and much less frequent than the previous species in our collections.
Synedra acus Kütz. Common in shallow waters at Yellowknife, Outpost and Gros Cap.
Synedra acus var. *radians* (Kütz.) Hust. Rare in shallow water at Yellowknife.
Synedra ulna (Nitzsch.) Ehr. This was the most common species of *Synedra*, found all over the main lake but not in McLeod and Christie Bays.
Synedra ulna var. *danica* (Kütz.) Grun. Taken only in the open water of Yellowknife Bay.
Synedra spp. Inshore samples in Yellowknife Bay.

Eunotiaceae

Eunotia lunaris (Ehr.) Grun. Common in Christie and McLeod Bays.
Eunotia pectinalis (Kütz.) Rab. Rare in shallow water at Outpost Island.
Eunotia praerupta Ehr. Common inshore at Outpost Island.

Achnanthaceae

Cocconeis pediculus Ehr. Rare at Yellowknife and Resolution.
Cocconeis placentula Ehr. Frequent in inshore collections all around the main lake.

Naviculaceae

Ahphiprora ornata Bailey. Rare in mid-lake, at Yellowknife and in the north arm.
Gyrosigma acuminatum (Kütz.) Rab. Rare, taken only in north arm.
Gyrosigma attenuatum (Kütz.) Cleve. Rare at Gros Cap and in north arm.
Gyrosigma kutzingii (Grun.) Cleve. Rare, taken only at Outpost Island.
Navicula cuspidata var. *ambigua* (Ehr.) Cleve. Rare at Gros Cap.
Navicula cryptocephala Kütz. Rare at Outpost and Resolution.
Navicula gastrum Ehr. Inshore tow at Resolution.
Navicula gracilis Ehr. Inshore at Outpost.
Navicula grevillei (Ag.) Cleve. Rare at Resolution.
Navicula lanceolata (Ag.) Kütz. Rare at Resolution.
Navicula oblonga Kütz. Inshore at Resolution.
Navicula placentula Ehr. Rare at Gros Cap.
Navicula pupula Kütz. Frequent at Outpost and Gros Cap.
Navicula radiosa Kütz. Common at Yellowknife, Gros Cap, Outpost and Resolution.
Navicula viridula Kütz. Outpost and Resolution.
Navicula spp. Several from Yellowknife Bay.
Neidium iridis (Ehr.) Cleve. Rare at Outpost.
Neidium productum (W. Smith) Cleve. Occasional at Gros Cap, Outpost and Resolution.
Pinnularia borealis Ehr. Rare at Outpost.
Pinnularia viridis (Nitzsch.) Ehr. Outpost and Gros Cap.
Stauroneis phoenicenteron Ehr. Only at Outpost.

Gomphonemataceae

Gomphonema geminatum (Lyngb.) Ag. Rare, taken only at Outpost Island.

Cymbellaceae

Amphora ovalis Kütz. Inshore only at Outpost, Gros Cap and Resolution.
Cymbella aspera (Ehr.) Herib. Rare at Outpost.
Cymbella cistula (Hemp.) Grun. Common at Outpost and Resolution.
Cymbella cuspidata Kütz. Inshore at Outpost and Gros Cap.
Cymbella cymbiformis (Kütz.) Cleve. Open water only, Yellowknife Bay.
Cymbella ehrenbergii Kütz. Rare, Gros Cap only.
Cymbella lanceolata (Ehr.) Kütz. At Yellowknife, Gros Cap and Outpost. This was the most common species of Cymbella in Great Slave Lake.
Cymbella tumida (Bréb.) Van Heurck. Outpost only.
Cymbella ventricosa Ag. Inshore at Outpost and Resolution.
Cymbella sp. Open water of Yellowknife Bay.
Epithemia argus Kütz. Rare at Outpost and Gros Cap.
Epithemia hyndmanni W. Smith. Outpost only.
Epithemia turgida (Ehr.) Kütz. Occasional at Resolution and Outpost.
Epithemia zebra (Ehr.) Kütz. One collection at Outpost.
Rhopalodia gibba (Ehr.) O. Muller. Frequent in shallow water at Yellowknife, Outpost and Gros Cap.
Rhopalodia gibba var. *ventricosa* (Ehr.) Grun. Rare at Outpost, Gros Cap and Resolution.

Nitzschiaceae

Hantzschia amphioxys (Ehr.) Grun. Rare at Resolution and Outpost.
Nitzschia sigma (Kütz.) W. Smith. Rare, taken only in shallows at Fort Rae.
Nitzschia sigmoidea (Ehr.) W. Smith. Occasional in north arm, Gros Cap and Outpost.
Nitzschia tryblionella Hantzsch. Only in shallows at Resolution.
Nitzschia vermicularis (Kütz.) Grun. Several collections at Outpost Island.

Surirellaceae

Campylodiscus hibernicus Ehr. Rare, taken only at Outpost.
Cymatopleura elliptica (Bréb.) W. Smith. Shallow water only, at Outpost.
Cymatopleura solea (Bréb.) W. Smith. Frequent in many collections from localities around the main lake.
Denticula tenuis var. Kütz. Rare, taken only at Outpost Island.
Surirella biseriata Bréb. Rare at Outpost and found also in Christie Bay.
Surirella ovalis Bréb. Common in hauls in shallow and deep water all over the main lake.
Surirella splendida (Ehr.) Kütz. In one sample at Gros Cap.

DIVISION PYRROPHYTA

Dinophyceae

Ceratium hirundinella (O.F.M.) Schrank. Widespread throughout the lake including Christie but not McLeod Bay.
Peridinium tabulatum (Ehr.) Clap. and Lachm. Rare, in Yellowknife Bay.

DIVISION CYANOPHYTA

Myxophyceae

Chroococcaceae

Chroococcus limneticus Lemm. Common in the north arm, Gros Cap and Outpost. Rare in Christie Bay.
Chroococcus turgidus (Kütz.) Naeg. Rare at Outpost and in Christie Bay.
Coelosphaerium naegelianum Ung. Rare, taken only at Outpost Island.
Coelosphaerium kuetzingianum Naeg. Rare in the north arm and at Outpost.
Gomphosphaeria aponina Kütz. Frequent in the north arm and rare at Resolution and in Christie Bay.
Gomphosphaeria lacustris Chod. Rare in the north arm.
Merismopedia elegans A. Br. Rare at Outpost Island.
Merismopedia glauca (Ehr.) Naeg. Occasional at Outpost and Resolution.
Merismopedia punctata Meyen. Frequent at Outpost Island.
Merismopedia tenuissima Lemm. Rare at Outpost Island.

Oscillatoriaceae

Oscillatoria limosa (Roth) Ag. In two shallow collections at Resolution.
Oscillatoria tenuis Ag. Occasional at Resolution, Gros Cap, Outpost and Yellowknife Bay.

Nostocaceae

Anabaena flos-aquae (Lyngb.) Bréb. Common at various points in the main lake, rare in Christie Bay. Not found in McLeod Bay.
Anabaena lemmermanni P. Richter. Frequent in the main lake and Yellowknife Bay.
Anabaena spiroides Kleb. Rare, at Outpost Island.
Aphanizomenon flos-aquae (L.) Ralfs. Frequent at Outpost, Gros Cap and Yellowknife Bay.

DIVISION RHODOPHYTA

Rhodophyceae

Adouinella sp. Fragments only from inner Bay at Yellowknife.

As usual, most of the phytoplankton species are cosmopolitan, occurring over wide areas in this and other continents. Nearly all the 160 species listed above have been found by Prescott (personal communication) in Alaska, at least 80% of them are known from the Great Lakes area, 80% in Scandinavia and 70% in Britain.

The Zooplankton

The identification of zooplankters has been made or confirmed by several specialists to whom the writer is greatly indebted. They are indicated under the headings for the appropriate groups. Aside from the moderate number of inshore samples referred to above, no special effort has been made to collect all the species of zooplankters occurring in the area. Neither has there been any thorough search of the collections on hand for rare specimens. Thus it is expected that the following list will be greatly extended by future studies.

PROTOZOA

Codonella cratera Leidy. Common and even abundant at open water stations throughout the main lake. Rare in McLeod and Christie Bays. Note that several genera, *Dinobryon*, *Mallomonas*, *Ceratium* and *Peridinium*, frequently considered as protozoans, have been listed above under the algal families Chrysophyceae and Dinophyceae.

ROTATORIA

For identification of the rotifers the author is greatly indebted to Dr. W. T. Edmondson of the University of Washington at Seattle.

Asplanchna priodonta Gosse. One of the six most abundant and widespread species. Found in all parts of the lake, sometimes very numerous (pulses).

Cephalodella gibba (Ehr.). Shallow water at Outpost Island.

Conochilus unicornis Rouss. Widespread, much more abundant in Christie Bay than in main lake.

Euchlanis dilatata Ehr. Inshore at Yellowknife and Resolution.

Euchlanis deflexa (Gosse). Inshore at Yellowknife only.

Gastropus stylifer Imhof. Common at Gros Cap.

Kellicottia longispina (Kell.). Second in abundance and a very widespread species especially in the east arm.

Keratella cochlearis (Gosse). The most numerous rotifer in the open water, widespread and of steady occurrence.

Keratella quadrata (Müll.). Common in most of lake except the east arm. Much less frequent than *K. cochlearis*.

Keratella earlenae Ahlstrom. Infrequent at Yellowknife and Gros Cap.

Lecane sp. Shallows at Outpost Island.

Monostyla sp. Inshore at Resolution.

Mytilina brevispina (Ehr.). Shallow water at Outpost Island.

Notholca squalmula (Müll.). Shallow water at Outpost Island.

Notholca labis Gosse. Gros Cap only.

Ploesoma hudsoni Imhof. Yellowknife, shallows only.

Ploesoma truncata Levander. Frequent inshore at Yellowknife and Outpost and Resolution.

Polyarthra major (Burck.). Generally abundant and one of the six major genera.

Polyarthra remata (Skorikow.). Occasional at Resolution and Gros Cap.

Polyarthra vulgaris Carlin. Inshore at Yellowknife.

Polyarthra sp. Occasional at Yellowknife and Resolution.

Synchaeta stylata Weirzejski. Very common at Yellowknife and Gros Cap, less common in the east arm.
Synchaeta spp. Frequent in main lake and east arm.
Trichocerca carinata Lamarck. Shallow water at Outpost.
Trichotria intermedia Bergendahl. Shallow water at Resolution.
Trichotria pocillum (Müll.). Shallow water at Outpost.

COPEPODA

The writer is grateful for identifications of various Entomostraca by Dr. J. E. Moore, University of Alberta, Edmonton, Dr. G. C. Carl, Provincial Museum, Victoria, and Dr. R. R. Langford, University of Toronto.

Diaptomus tenuicaudatus Marsh. Widespread in the open water.
Diaptomus sicilis Forbes. Also widespread, and considered by most authorities to be inseparable taxonomically from *D. tenuicaudatus*.
Diaptomus ashlandi Marsh. Moderate numbers, especially at Outpost.
Diaptomus minutus Lilljeborg. Common in many localities.
Diaptomus tyrelli Poppe. Occasional, at Gros Cap.
Limnocalanus macrurus Sars. Widespread and numerous.
Senecella calanoides Juday. Found at most deep water stations in the main lake and more numerous in the east arm.
Epischura lacustris Forbes. Irregular in distribution and less common in the deeper water.
Cyclops strenuus Fischer. Very common, especially in the east arm.
Cyclops bicuspidatus Claus. Widespread.
Cyclops viridis brevispinosus Herrick. Common in shallow water areas.
Cyclops scutifer Sars. Few in the east arm.
Moraria duthiei Scott. (Identified by Dr. R. E. Coker, University of North Carolina.) This harpacticoid species was rare in shallow water at Yellowknife Bay, and apparently the same species at Outpost Island.

CLADOCERA

Daphnia longispina (O. F. Müller). Widespread and numerous, common in the east arm.
Daphnia pulex (de Geer). Mostly from inshore collections, rarely numerous, but common at Outpost Island.
Sida crystallina (O.F.M.). Rare in Great Slave but collected also in Artillery Lake and Lake Athabasca.
Diaphanosoma brachyurum (Lieven). Few specimens from McLeod Bay and near Fort Rae.
Bosmina obtusirostris Sars. Common especially in late summer. Rare in east arm.
Chydorus sphaericus (O.F.M.). Rare, in collections from Gros Cap.
Polyphemus pediculus (L.). Rare at Gros Cap and Outpost.
Leptodora kindtii (Focke). Few, but widespread; common in Inconnu Channel.
Alona affinis (Leydig). Rare and only in shallow water.
Holopedium gibberum Zaddach. Rare at Gros Cap but frequent in east arm and Artillery Lake.
Simocephalus vetulus (O.F.M.). Common in shallows at Outpost Island.

WEIGHT OF THE PLANKTON CROP

The main effort toward measuring the standing crop of net plankton involved taking, with the large net, many total vertical hauls in all parts of the lake and at different times throughout the season. These were later dried, weighed and ashed to determine the weight of organic matter as described above. The gravimetric data from most of the stations for the years 1944–1947 are assembled

in Table II. The extensive data from Station 31, off Gros Cap, for the years 1946 to 1954 are presented in Table III. In these tables, the dry weight and organic matter given are those of the total vertical haul on the dates indicated. The equivalent dry weight in kilograms per hectare is calculated from the amount of the total vertical haul using the average efficiency factor of 37% as explained above. In assembling these data a small number of determinations in which the sample showed contamination with silt, were omitted. Such contamination occurred occasionally when the net assembly touched and stirred up bottom deposits. *Mysis relicta* was removed from the plankton sample before drying. From one to six of these organisms occurred in about one-quarter of the total vertical hauls. It is debatable whether *Mysis* should be considered as part of the plankton but the erratic nature of its occurrence suggested that the best procedure was to remove it. The distribution of *Mysis* in Great Slave Lake has been described by Larkin (1948).

TABLE II.—Gravimetric analysis of plankton samples from Great Slave Lake (except Station 31) 1944 to 1947.

Sta. No.	Date	Dry wt.	Organic matter		Dry wt.	Sta. No.	Date	Dry wt.	Organic matter		Dry wt.
		mg.	*mg.*	%	*kg./ha.*			*mg.*	*mg.*	%	*kg./ha.*
	1944										
1	June 23	26.8	8.2	31	14.7	8	July 27	48.7	38.8	80	27.3
2	June 25	18.7	11.6	62	10.6	11	Aug. 7	43.2	23.3	54	23.7
3	June 26	28.6	16.5	58	15.8	13	Aug. 15	20.5	15.8	77	11.3
4	June 27	16.5	9.4	57	9.1	5	Aug. 25	87.7	73.9	84	48.2
5	June 29	28.2	18.2	65	15.5	15	Aug. 28	15.8	11.8	75	8.7
5	July 14	59.8	36.3	61	32.9						
	1945										
5	July 16	19.2	12.3	64	10.6	24	July 1	19.2	8.3	43	10.6
7	July 14	32.3	16.1	50	17.8	25	July 24	34.5	18.2	53	19.0
18	July 5	52.1	37.4	72	28.6	26	July 30	20.8	11.8	52	11.4
18	July 27	24.4	17.0	70	13.4	27	Aug. 2	28.0	12.2	44	15.4
19	July 11	26.3	9.7	37	14.5	28	Aug. 8	14.1	10.7	76	7.8
19	Aug. 23	23.4	12.1	52	12.9	29	Aug. 13	15.9	12.3	77	8.7
21	July 11	34.1	10.7	31	18.7	30	Aug. 18	21.7	14.5	67	11.9
22	July 10	26.9	14.2	53	14.8						
	1946										
1	June 16	14.6	5.1	35	8.0	42	Aug. 21	28.5	24.6	86	15.7
2	June 17	29.4	9.5	32	16.2	35	July 3	11.6	9.5	82	6.4
5	July 29	65.1	30.6	47	35.8	35	July 18	10.9	8.8	81	6.0
5	Aug. 10	39.4	29.5	75	21.7	35	Aug. 1	22.4	19.2	86	12.3
32	June 18	17.5	8.9	51	9.6	35	Aug. 18	37.7	31.9	85	20.7
33	June 22	35.7	17.1	48	19.6	35	Aug. 30	78.0	67.1	86	42.9
37	July 13	70.2	22.2	32	38.6	36	July 5	10.7	3.6	34	5.9
38	July 18	53.2	28.9	54	29.3	36	July 19	14.1	8.7	62	7.7
39	July 29	36.7	32.0	87	20.2	36	Aug. 4	37.2	30.5	82	20.5
40	Aug. 6	69.0	51.1	74	38.0	36	Aug. 19	64.7	56.2	87	35.6
	1947										
2	July 7	24.0	10.6	44	13.2	35	July 11	16.8	13.1	78	9.2
5	July 29	30.0	21.0	70	16.5	35	July 17	12.7	10.4	82	7.0
45	July 19	15.0	10.5	70	8.2	35	Aug. 13	42.0	33.8	80	23.1
55	Aug. 7	46.8	36.1	77	25.7	35	Aug. 21	14.7	8.2	56	8.1
56	Aug. 7	54.0	45.6	84	29.7	36	July 12	22.1	15.9	72	12.1
57	Aug. 7	52.0	28.8	55	28.6	36	July 18	13.5	10.1	75	7.4
						36	Aug. 14	10.6	7.6	72	5.8

TABLE III.—Gravimetric analysis of total vertical net plankton samples from Station 31 off Gros Cap, Great Slave Lake, 1946 to 1954.

Date	Dry wt. per haul	Organic matter		Dry wt.
	mg.	*mg.*	%	*kg./ha.*
1946				
June 17	33.5	16.1	48	18.4
June 23	46.3	24.0	52	25.5
July 1	56.5	23.2	41	31.1
July 7	42.1	13.9	33	23.1
July 14	39.0	35.1	90	21.4
July 21	23.7	20.5	87	13.0
July 28	64.0	51.2	80	35.2
Aug. 3	16.3	11.2	69	9.0
Aug. 19	45.6	34.7	76	25.1
Aug. 27	24.1	14.0	58	13.2
Sept. 2	41.3	30.4	73	22.7
Average				21.6
1947				
June 25	9.1	6.1	67	5.0
July 3	21.6	12.3	57	11.9
July 9	47.5	16.6	35	26.1
July 17	73.5	36.1	49	40.4
July 23	28.7	15.6	54	15.8
Aug. 5	24.0	7.9	33	13.2
Aug. 12	23.1	10.6	46	12.7
Aug. 22	63.8	44.2	70	35.1
Aug. 27	41.2	25.8	63	22.7
Sept. 2	50.6	40.4	80	27.8
Sept. 9	45.5	30.4	67	25.0
Sept. 21	49.4	32.4	65	27.2
Average				21.9
1948				
June 26	46.0	35.1	76	25.3
July 1	51.6	44.8	87	28.4
July 8	22.2	16.2	73	12.2
July 14	25.5	21.3	84	14.0
July 22	35.3	31.7	90	19.4
July 31	24.0	15.9	66	13.2
Aug. 6	42.0	32.6	78	23.1
Aug. 11	24.3	16.1	66	13.4
Aug. 26	49.2	40.5	82	27.0
Sept. 11	65.7	55.3	84	36.1
Average				21.2
1949				
June 21	36.1	21.1	58	19.8
July 11	24.8	19.8	80	13.6
July 25	52.4	40.4	77	28.8
Aug. 11	64.9	59.9	92	35.7
Average				24.5
1950				
July 4	32.6	21.5	66	17.9
July 21	40.5	28.0	69	22.2
Aug. 10	19.8	12.7	64	10.4
Aug. 23	27.6	18.7	68	15.1
Average				16.4
1951				
July 17	40.9	26.6	65	22.5
Aug. 5	28.8	19.8	68	15.8
Aug. 10	61.1	50.7	83	33.6
Aug. 31	40.2	34.9	87	22.1
Average				23.5
1952				
July 13	32.7	26.8	82	18.0
July 22	91.5	57.5	63	50.3
Aug. 4	26.7	18.8	70	14.7
Aug. 11	15.7	11.1	72	8.6
Aug. 22	28.1	24.3	86	15.4
Sept. 1	37.3	31.4	84	20.5
Average				21.1
1953				
July 13	37.2	24.2	65	20.4
July 25	81.1	68.4	84	44.6
Aug. 8	26.4	19.6	74	14.5
Aug. 19	35.6	28.8	81	19.6
Sept. 1	14.0	10.1	72	7.7
Average				21.3
1954				
July 3	56.1	16.3	29	30.8
July 11	76.2	26.6	35	41.8
July 17	58.6	34.6	59	32.2
July 26	37.5	23.6	63	20.6
Aug. 2	27.8	28.0	74	15.3
Aug. 9	43.2	34.5	78	23.7
Aug. 16	55.8	43.0	77	30.7
Aug. 24	116.0	93.8	81	63.8
Sept. 3	24.1	18.3	76	13.3
Sept. 11	27.6	16.6	61	15.2
Sept. 15	55.2	38.6	70	30.4
Average				28.9

The information presented in Tables II and III must be analysed to decide on representative values for the weight of plankton in the whole lake and in its parts. A first examination of the data shows that McLeod and Christie Bays have consistently lower standing crops than the remainder of the lake. If we exclude these bays, there are left 104 determinations from the remainder of the lake which average 21.8 kg. dry weight of plankton per hectare. Since the main lake includes parts varying greatly in depth, protection and geological surroundings,

it may well be questioned whether the plankton can be represented by an average value. Dividing the 104 samples into geographical regions the following picture emerges:

Station 31, off Gros Cap	– 67 samples–Average	23.7 kg./ha.
Open lake	– 9 samples–Average	25.1 kg./ha.
Yellowknife Bay	– 9 samples–Average	23.3 kg./ha.
Near Outpost Island	– 7 samples–Average	17.4 kg./ha.
Resolution	– 6 samples–Average	12.0 kg./ha.
Islands area and north arm	– 6 samples–Average	17.4 kg./ha.

The general agreement between the average amount of plankton at Station 31 and that of the open lake is gratifying since this station was selected in the hope that it would prove representative of the main lake. Yellowknife Bay is somewhat cut off from the main lake and was found to be warmer (Rawson 1950) and to have a heavier bottom fauna (Rawson 1953a). The low averages of the Outpost Island, Resolution and Islands areas are primarily related to the large number of shallow stations sampled in these areas. In the Resolution area another factor was the circumstance that most of these samples were taken soon after the break-up of the ice and before the plankton had time for much development.

The average amount of plankton from samples in Christie Bay was 14.3 kg./ha. and in McLeod Bay 9.0 kg./ha. In an earlier paper (Rawson 1953a) the value of 10.6 was listed for Christie Bay. This is now corrected (to 14.3) by the inclusion of rich samples not analysed when the former average was calculated. The low plankton crop in the east arm and particularly its scarcity in McLeod Bay, will be cited below as evidence of the extreme oligotrophy of these parts of the lake. Christie Bay, although twice as deep as McLeod Bay, has a considerably heavier plankton crop. This was suggested (Rawson 1953a) as evidence of an edaphic effect, since McLeod Bay has only one-fifth the mineral content of Christie Bay. Great Bear Lake was not included in Figure 6 below since the writer had only three total vertical hauls provided by Dr. R. B. Miller in 1945. However the average of these was 22 mg. dry weight, equivalent to 12 kg./ha. This lies between the amounts found in McLeod and Christie Bays. The mineral content of the water of Great Bear Lake is also intermediate between that of McLeod and Christie Bays (Rawson 1951a).

The plankton crop has been expressed above in terms of weight per unit area rather than per unit of volume. This procedure eliminates the difficulty of uneven vertical distribution of plankton through the column of water strained. There remains, however, the problem that the sampling stations are in different depths and some of them are in water too shallow to support a "full" crop of plankton. Using the data in Tables II and III and plotting the amounts of plankton against the depth of the stations as shown in Table I, it is found that no station less than 30 metres deep had a plankton crop greater than 20 kg./ha. while the deeper stations often had crops of 30 to 60 kg./ha. It was thus of interest to test the vertical distribution of plankton in various parts of the lake.

A preliminary check on vertical distribution was made by taking vertical series of stage hauls with a closing net and centrifuging these in graduated tubes

to obtain the relative volumes of plankton in the different strata. It is obvious that any accurate determination of vertical distribution would require much sampling in order to cope with the extensive diurnal migrations of the zooplankters. Four vertical stage series were taken at the deepest station, No. 36 (in Christie Bay). The vertical distribution of plankton at this station on four dates is shown in the graph, Fig. 5, and the average vertical distribution expressed as percentage of the total hauls was as follows:

0–10 metres—56%	50–100 m.—7.0%	300–400 m.—0.5%
10–25 metres—17%	100–200 m.—1.0%	400–500 m.—0.4%
25–50 metres—17%	200–300 m.—1.0%	500–600 m.—0.6%

Vertical distribution at Station 35, also in Christie Bay but only 140 metres in depth, was tested on two occasions in 1947. The average of these determinations was as follows:

0–10 m.—49%	25– 50 m.—14%	100–135 m.—8%
10–25 m.—10%	50–100 m.—18%	

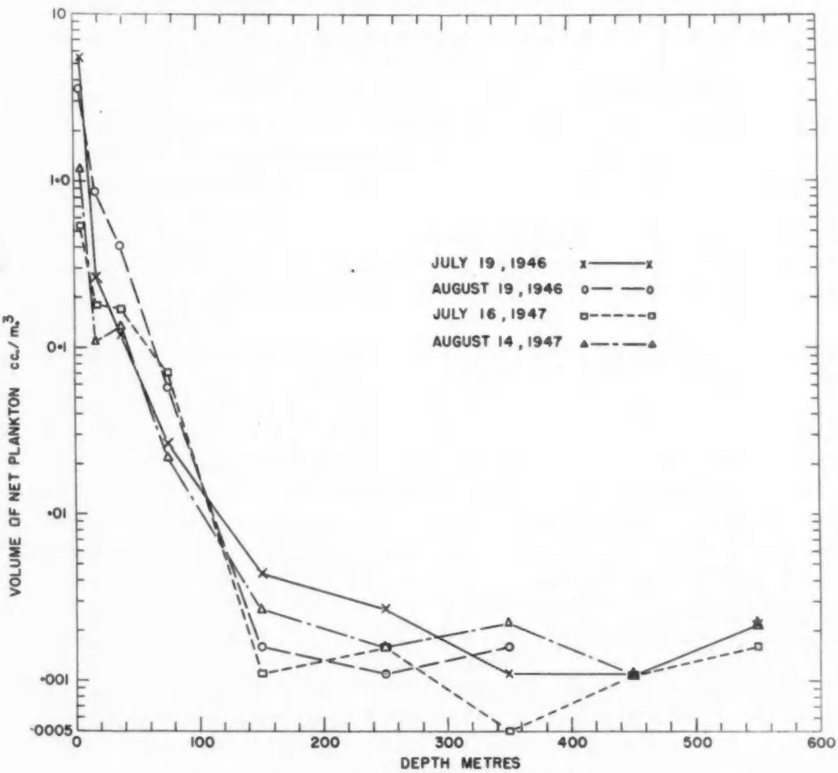

FIG. 5.—Vertical distribution of net plankton measured volumetrically on four dates at Station 36, Christie Bay, Great Slave Lake.

Four similar determinations were made in the main lake, two at Station 4 off Gypsum Point, June 27, 1944, and two at Station 31 off Gros Cap on July 17, 1947. The average vertical distribution of plankton by volume at these two stations was as follows:

Station 31	*Station 4*
0–10 m.—42%	0–10 m.—36%
10–25 m.—17%	10–25 m.—17%
25–50 m.—21%	25–50 m.—14%
50–94 m.—20%	50–100 m.—22%
	100–140 m.—12%

Evidently in Great Slave Lake the bulk of the plankton (50–70%) is commonly found in the upper 25 metres. A further amount of 15–20% is usually between 25 and 50 metres and from 7 to 20% between 50 and 100 metres. In areas deeper than 100 metres there is a significant amount of plankton below the

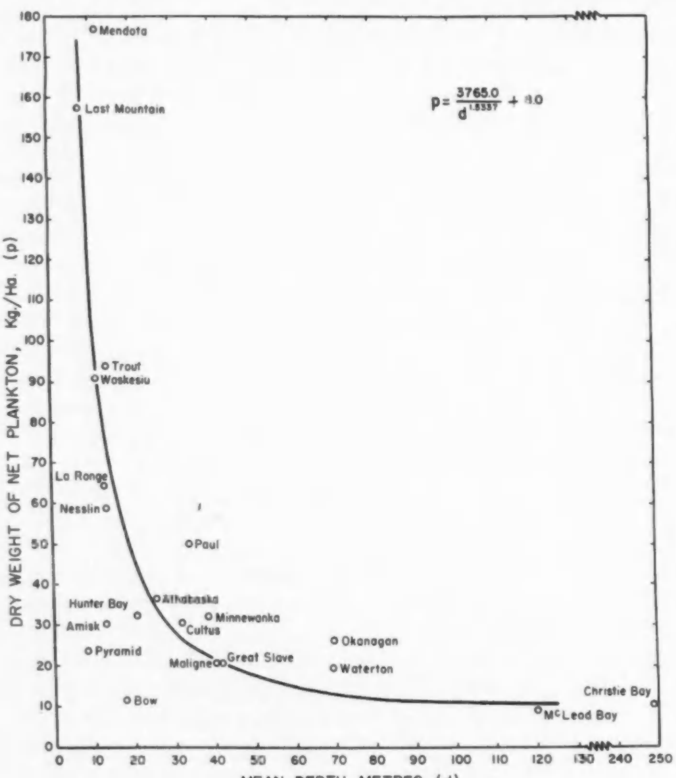

FIG. 6.—Mean depth and the standing crop of net plankton in twenty lakes.

100-metre level but it rarely exceeds 10% of the total vertical haul. The numerical composition of the plankton at various depths is discussed in a later section.

The average standing crop of net plankton in the main part of Great Slave Lake was stated above as 21.8 kg. dry weight per hectare. This differs only slightly from the value of 20.3 kg./ha. quoted in an earlier paper (Rawson 1953a) and based on a smaller number of samples. In that paper the standing crop of net plankton in twenty large lakes of Western Canada was compared and related to the mean depth of these lakes. The graph, reproduced here as Fig. 6, presents the data which lead to the conclusion that morphometric influences are dominant in controlling the plankton production in these lakes. The isolated and very deep bays, McLeod and Christie, are treated as separate bodies of water in this comparison and the plankton crops for these areas fit very well into the general relationship.

SEASONAL AND ANNUAL VARIATION IN THE WEIGHT OF THE PLANKTON

Because of the known variability of plankton communities, frequent and long-continued sampling at specific stations are needed to determine the course and extent of seasonal variation in a plankton crop. In the years 1944 and 1945, the exploration of the whole lake precluded any such program although two or more visits were made to several stations when opportunity allowed. In 1946 it was possible to begin extensive sampling at Station 31 near Gros Cap. This was continued at approximately weekly intervals in the summers of 1946 to 1948 and at less frequent intervals from 1949 to 1954 (Table III). These data are the main source of our information on seasonal and annual change in the plankton of Great Slave Lake. Additional information was obtained from repeated sampling at a few other places, especially Station 5 in Yellowknife Bay and Stations 35 and 36 in Christie Bay.

Before attempting to discuss the annual and seasonal variations of plankton in the various years it is necessary to analyse the physical and chemical data which has been collected at Station 31 at the time of each plankton sampling. In the first three summers these data included a complete record of vertical temperatures, using a bathythermograph, determination of dissolved oxygen at suitable levels, and Secchi disc measurements of light penetration. Since the dissolved oxygen, even near the bottom, was usually more than 80% of saturation, this measurement was discontinued in the later years. Temperature and light penetration data are presented in Table A (Appendix) for 1946 to 1948 and in Table B for 1949 to 1954. The course of temperature change in each of these years is indicated by the graphs Fig. 7, 8 and 9 in which selected temperature curves are plotted from the data in Tables A and B.

In any attempt to relate plankton changes to water temperatures it will be desirable to have some scheme which describes the temperature of the lake and shows the progress of heating and cooling during each season. Such an index is not readily derived. Mean temperatures and heat budgets are of value in the physical description of lake conditions but they are affected by penetration of

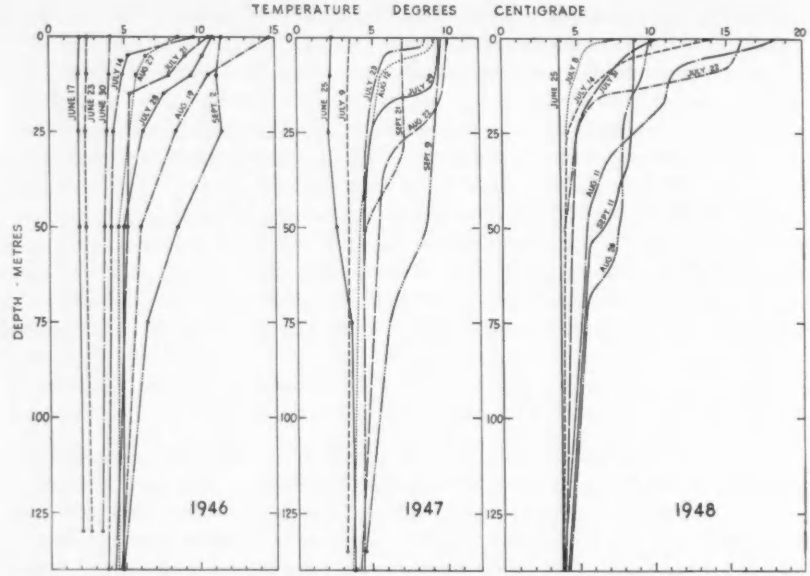

FIG. 7.—Selected temperature curves for the seasons 1946, 1947 and 1948 at Station 31, off Gros Cap.

heat into deep water whereas the plankton crop is most directly influenced by the mean temperature of the upper or trophogenic stratum. It was noted above that 70 to 80% of the Great Slave Lake plankton is found in the upper 25 metres. In smaller lakes of an alpine area the author (Rawson, 1942) found a relation between the mean temperature of the 0- to 10-metre zone and the average quantity of net plankton. In dealing with the present data from the central region of Great Slave Lake, mean temperatures of 0- to 10- and 0- to 25-metre strata have been investigated. No very useful results were obtained so we have continued with the procedure used in the earlier account of physical conditions in Great Slave Lake, calculating mean temperatures from the vertical temperature curves. These mean temperatures are weighted according to the percentage volume of the main lake found at the different levels, i.e. 0 to 25 metres, 50%; 25 to 50, 26%; 50 to 100, 22%; deeper than 100, 2%. This is obviously an artificial treatment since it takes no account of different rates of warming in other parts of the lake and since our so-called mean temperatures are affected by water movements as well as by actual heating. Nevertheless it provides a rough description of the progress of warming of the lake. The mean temperatures calculated from the data in Tables A and B are plotted in the graph Fig. 10. In this graph the curves for the first three years are smoothed by threes but in subsequent years the data were too few to justify this procedure. It is immediately evident that high lake temperatures were reached in the years 1948, 1949, 1951, 1953 and 1954; lower tempera-

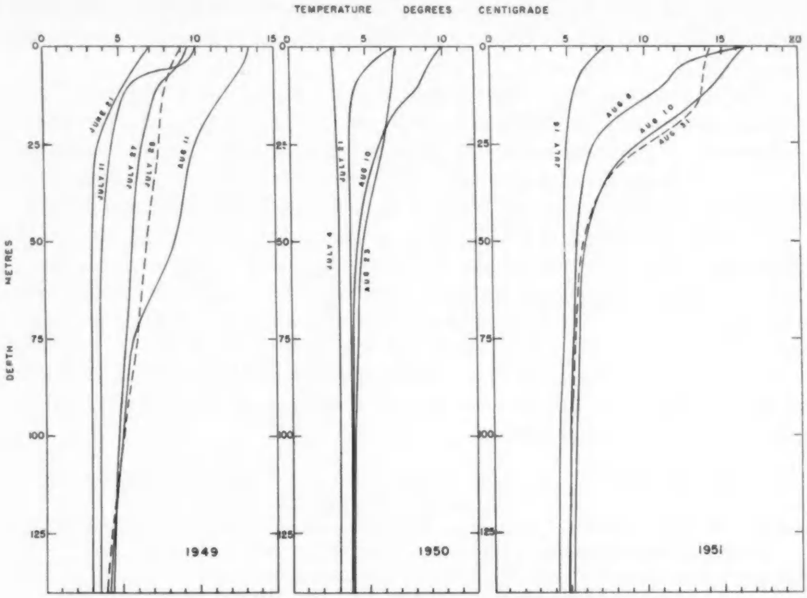

Fig. 8.—Selected temperature curves for the seasons 1949, 1950 and 1951 at Station 31, off Gros Cap.

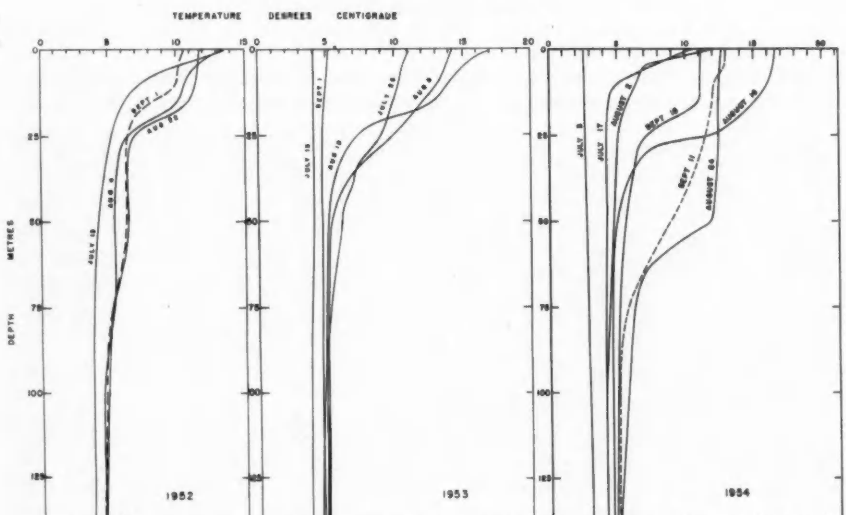

Fig. 9.—Selected temperature curves for the seasons 1952, 1953 and 1954 at Station 31, off Gros Cap.

tures prevailed in 1946, 1947 and 1950; and 1952 was somewhat intermediate. More specific reference to these curves will be made in discussing the plankton crop.

The information as to light penetration at Station 31 is recorded in the Secchi disc readings in Tables A and B and plotted in Fig. 11. The average transparency is about 4.5 metres. In June and early July it is usually higher than this, while in August and September it is usually lower. Two years stand out as exceptional. In 1950 the transparency remained high in late July and August. It is noteworthy that this was also the year of the coldest water (Fig. 10). In 1948 the transparency was extremely low from mid-July to mid-August. This was the result of unusual water movements which brought warm and muddy water 40 miles across the lake from the Slave River delta. Similar, but brief, occurrences were noted again on August 10, 1951, and August 9 to 16, 1954.

From the above data and from observations as to the breaking-up of the ice cover, it is possible to characterize the water climate at Station 31 in the nine summers of observation as follows:

1946—Ice off very early (June 5), water warming slowly, low temperature in mid-August.

1947—Ice off very late (June 23), warming slow, low temperature at mid-August.

1948—Ice off early (June 8), pronounced thermal stratification in July, warming to above average in August, muddy delta water present for a month.

1949—Ice off late (June 16), warming rapid to a high level at mid-August.

1950—Ice off late, warming very slow, lake coldest of the 9-year period.

1951—Ice off at average time, extensive warming in upper layers (0–25 m.) but less than average heat penetration. Brief influx of muddy water August 10.

1952—Ice off early, initial warming rapid then moderate temperatures in August.

1953—Ice off at average time, warming rapid to high temperatures at mid-August. Prolonged storms caused rapid cooling at end of August.

1954—Ice off at average time, early warming slow but high temperatures at mid-August. Extreme thermal stratification on August 16. Brief inflow of turbid water August 9 to 16.

The differences in the average annual crops of net plankton at Station 31 may be observed in Table III. These range from 16.4 kg./ha. in 1950 to 28.9 kg./ha. in 1954 with an average for the 9 years of 23.7 kg./ha. This is a remarkably small variation when one considers the results from other lakes and the climatic variations in the different years as indicated above. The average for the five "warm" summers 1948, 1949, 1951, 1953 and 1954 is 23.9. That for the three "cold" summers 1946, 1947 and 1950 is 19.9. Moreover the greatest average crop, 28.9 kg./ha., was in 1954 which had the highest mean temperatures (Fig. 10) while the lowest average crop, 16.4 kg./ha., was in 1950 which had the lowest mean temperatures for the 9-year period.

Variations in the plankton crop during the season are illustrated by the data for the summers 1946 to 1948 and 1952 to 1954, in Fig. 12. In these years the samples were taken at approximately weekly intervals. In 1949, 1950 and 1951 the samples were usually at intervals of 2 weeks or longer and the data are thus too meagre to reveal any clear pattern of fluctuation. This observation will be of interest, no doubt, to those who must decide on the frequency of sampling in a

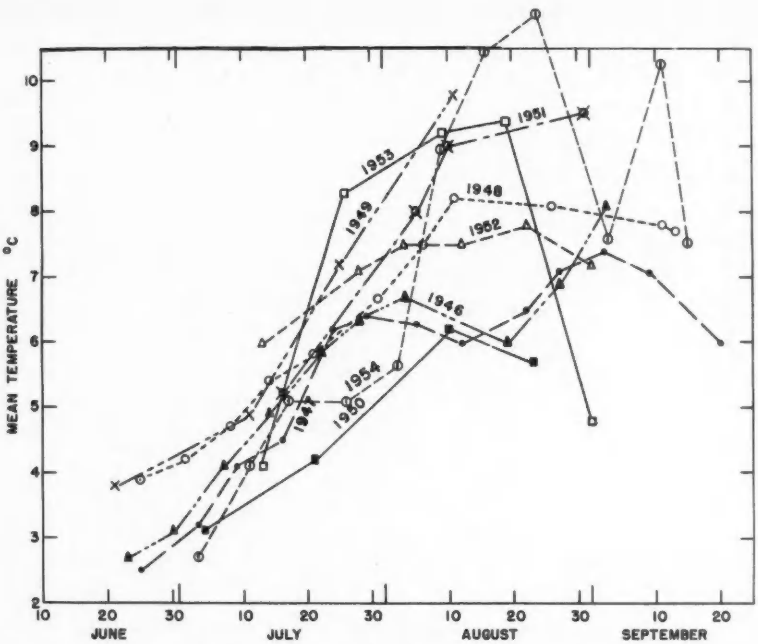

FIG. 10.—Mean lake temperatures at Station 31 for the years 1946 to 1954.

plankton program. In lakes of this kind, the desirable interval would appear to be less than one week if seasonal changes in abundance are to be followed. Nevertheless the annual averages resulting from less frequent sampling fall quite consistently near those obtained from weekly samples.

The amount of plankton at Station 31 varied widely during the six summers represented in Fig. 12. With few exceptions the amounts lie between 10 and 40 kg./ha. While the graph gives a general impression of erratic fluctuation, closer examination reveals some evidence of a seasonal pattern. Thus in each of the six years an early season maximum ranging between 30 and 50 kg./ha. occurs between July 1 and 28. This is followed by a sudden and drastic reduction in the amount of plankton, usually resulting in a minimum between August 1 and 15. Such a reduction to 15 kg./ha. or less, occurred in five of the six years illustrated in Fig. 12. The plankton increased again after August 15 but frequently suffered another decrease in late August or early September. In five of the six years the plankton was increasing toward the last date of sampling and in the remaining year, 1953, sampling was terminated too early (September 1) to discover whether an autumn increase occurred.

The major discrepancies from the general pattern described above were found in the years 1946 and 1948. In 1946 an early maximum plankton was observed on July 1 followed by a marked decrease and a second maximum at

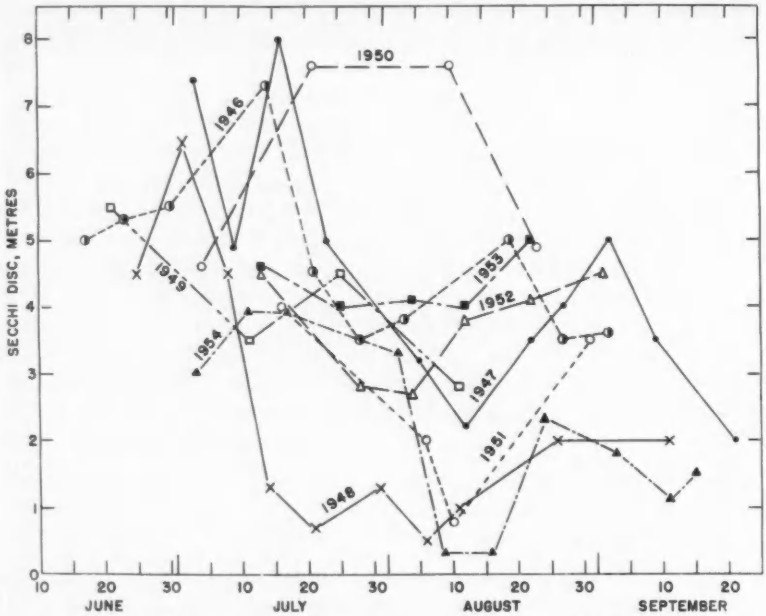

FIG. 11.— Secchi disc readings at Station 31 for the years 1946 to 1954.

July 28 (Fig. 12). The unusually early break-up of ice and high mean water temperatures at mid-June (Fig. 10) would seem to be related to this "extra" maximum. The season of 1948 started off much like 1946 and an early plankton maximum was observed on July 1. However, in spite of steady warming, the plankton crop deteriorated and did not recover beyond 23 kg./ha. until late August. Since mean water temperatures were fairly high in July and August, this would seem to run counter to the observation that high mean temperatures were accompanied by heavy plankton crops. Turning to Fig. 11, it will be seen that in mid-July 1948, the transparency of the water dropped to an unprecedented low point and remained down through the mid-summer period. The excessive turbidity was caused by an inflow of muddy water from the Slave River Delta, 40 miles south. This condition would appear to be the cause for the poor growth of plankton at Station 31 in midsummer of 1948. Again in September 3 to 11, 1954, the arrival of muddy water and lowered light penetration was accompanied by a sharp and extensive drop in the quantity of plankton (Fig. 12).

The early-summer maximum and subsequent midsummer reduction, shown in Fig. 12, are presumably related to seasonal changes in factors such as water temperature and light. Since the seasons vary from year to year there would seem to be no good reason why the events should be fitted to a single calendar scale. Thus if the curves in Fig. 12 are shifted so that the main early summer maxima coincide, a much more convincing "phenological" trend emerges. Such a pro-

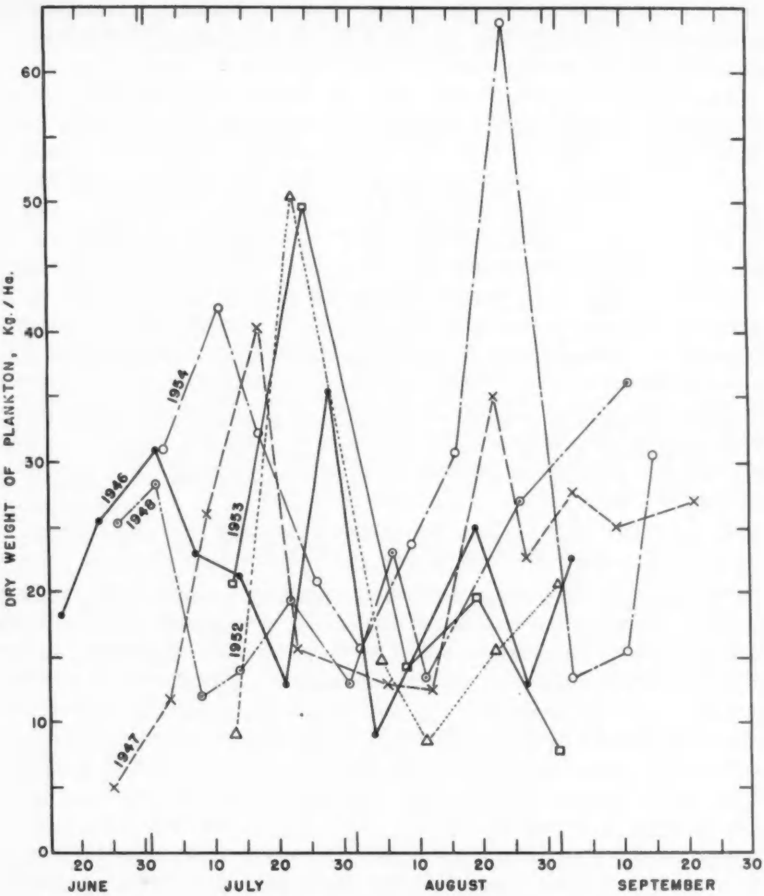

FIG. 12.—Dry weight of net plankton per unit area through six summers at Station 31, Great Slave Lake.

cedure shows that the midsummer period of low production usually lasts for about 3 weeks, whereas the overlapping curves in Fig. 12 almost mask its existence.

The annual growth season for plankton in Great Slave Lake is greatly restricted by its short ice-free period, roughly June 10 to mid-December. Thus the early period of plankton abundance has been called early summer rather than the more usual "spring" maximum. In Christie Bay of the east arm, the ice-free period is approximately one month shorter than that at Station 31. In 1946 no early summer maximum or midsummer minimum were evident in this area. The amount of plankton in the east arm tended to increase in a fairly regular way to

maxima in late August. In 1947 the low crop in mid-August suggests a midsummer minimum. It is unfortunate that we were not able to observe the plankton of the east arm for a longer period.

The selection of Station 31, off Gros Cap, for continued sampling was made partly because it is close to the geographical centre of the lake and partly because it could be reached quickly from the commercial fishing base in the Gros Cap Channel. Since we have much less extensive data from other stations for comparison we can only speculate as to whether it was a good choice. It was indicated above that the 9-year average standing crop of net plankton at Station 31 was 23.7 kg. dry weight per hectare. The average from other stations is 21.8 kg./ha. and this value is somewhat depressed by the inclusion of several shallow stations. Thus the amount of plankton at Station 31 may be considered as representative of the main lake. Observations of the physical and chemical conditions at Station 31 show somewhat erratic changes resulting from large-scale cold water movements from the Hearne Channel to the east and, on rare occasions, of warm water from the delta region to the south. It is possible, therefore, that a station farther out into the central portion of the main lake might have shown less variation in its plankton crop.

NUMERICAL ANALYSIS OF THE PLANKTON

All of the plankton samples were subjected to a preliminary qualitative examination during which notes were made as to the species present and their relative abundance. This proved helpful in indicating distribution, especially of those species which appear irregularly and not in significant numbers for the numerical analysis. In the counting procedures described above it was frequently impossible to identify to species the large numbers of *Diaptomus, Cyclops,* and other dominant genera of plankters. The qualitative examinations provided data as to the relative abundance of numerous species and was the source of annotations in the foregoing lists. In the following sections numerical abundance will be considered first in the main lake, relying mainly on data from the centrally located Station 31. The need for long-continued sampling of plankton populations has been emphasized by D'Ancona (1955) in his discussion of the stability of plankton communities. The less extensive materials from other areas of Great Slave Lake are useful for comparison. The plankton of the east arm differs both in quantity and quality so it will be considered later.

Plankton of the Main Lake

An introduction to the numerical composition of the net plankton of Great Slave Lake can be obtained by examining Tables IV and V which summarize the data from Station 31 for 7 years. Samples for the years 1949 and 1950 were few in number and unsuitable for counting since they were preserved in weak alcohol. Table IV shows that the average total vertical haul brought up about 6,800 entomostracans, 3,300 rotifers and 10,300,000 cells of phytoplankters. Phytoplankter cells thus outnumber zooplankter individuals by about 1000 to 1 but

TABLE IV.—Summary of the annual average numbers of plankters, also percentage of volumes (in parentheses), and ratios of phytoplankton to zooplankton volumes, in total vertical hauls at Station 31, Great Slave Lake for 7 years. (Note that numbers per total vertical haul in this and succeeding tables may be converted to numbers per square metre by multiplying by 55.)

	Entomostraca	Rotifers	Total zooplankters	Total phytoplankters (cells)	Phytoplankton: zooplankton ratio, by volume
1946	8,339 (91.8)	1,903 (2.6)	10,242 (94.4)	8,133,000 (5.6)	1 : 17
1947	4,827 (92.8)	3,469 (2.6)	8,296 (95.4)	8,659,000 (4.5)	1 : 21
1948	7,633 (97.8)	1,429 (0.8)	9,062 (98.6)	4,085,000 (1.4)	1 : 70
1951	4,840 (90.2)	1,260 (3.2)	6,100 (93.4)	9,650,000 (6.6)	1 : 14
1952	7,112 (67.5)	5,340 (29.5)	12,452 (97.0)	6,911,000 (3.0)	1 : 32
1953	5,844 (71.0)	5,292 (26.9)	11,136 (97.9)	5,092,000 (2.1)	1 : 47
1954	8,949 (87.4)	4,441 (0.5)	13,390 (87.9)	29,723,000 (12.1)	1 : 7
7-year average	6,792 (85.5)	3,305 (9.5)	10,097 (95.0)	10,322,000 (5.0)	1 : 19

in volume the animals exceed the plants by 19 to 1. The relative abundance of various genera in the three main groups of plankters is shown in Table V which gives the average percentage composition for each of 7 years and for the whole period.

Nauplii make up nearly 50% of the Entomostraca counts and, since they are the young of the three copepod genera which follow (in Table V), the true percentage of the five genera is approximately twice that recorded. *Diaptomus* is by far the most numerous entomostracan, contributing about one-third of the total count, *Cyclops* follows with about 10% and *Limnocalanus* with 5%. It may be interjected that the volume of *Limnocalanus* averages about tenfold that of *Cyclops*

TABLE V.—Average percentage composition by numbers of three groups of plankters in total vertical hauls at Station 31, Great Slave Lake, in 7 years.

	1946	1947	1948	1951	1952	1953	1954	7-year average
				ENTOMOSTRACA				
Nauplii	57.0	44.9	51.5	36.3	61.9	44.6	35.3	47.3
Diaptomus	27.6	33.2	29.6	46.4	24.1	39.9	45.4	35.3
Cyclops	10.8	14.4	12.4	11.1	7.4	9.3	11.1	10.9
Limnocalanus	3.9	6.2	5.7	4.9	6.2	6.0	6.0	5.5
Daphnia	0.5	0.3	0.2	0.2	0.3	0.2	1.5	0.5
Bosmina	—	0.8	0.5	0.2	0.1	—	0.7	0.3
				ROTIFERS				
Keratella	26.8	52.9	34.0	38.5	24.3	29.4	58.0	37.8
Kellicottia	20.9	26.1	41.7	40.2	17.2	17.8	21.2	26.3
Synchaeta	42.3	13.5	12.5	3.9	17.0	18.4	0.6	15.5
Asplanchna	6.1	2.3	1.5	10.0	36.6	31.1	12.3	14.3
Polyarthra	3.9	5.2	10.2	7.4	4.9	3.4	7.7	6.0
				PHYTOPLANKTERS				
Melosira	74.5	70.3	82.5	78.8	54.7	65.4	89.0	73.6
Asterionella	7.7	25.5	10.9	11.1	26.0	20.2	7.4	15.5
Fragilaria	1.7	1.7	4.8	2.1	0.2	12.7	0.5	3.4
Tabellaria	4.4	0.1	0.7	—	3.5	0.8	1.6	1.6
Synedra	0.5	0.1	0.1	—	0.1	0.1	—	0.1
Anabaena	0.2	1.9	0.5	2.5	1.2	0.1	0.1	0.9
Dinobryon	10.7	0.3	0.4	5.5	14.2	0.7	1.3	4.7

or *Diaptomus* so it is actually the largest component of the plankton. The two cladocerans, *Daphnia* and *Bosmina* contribute only insignificant numbers (less than 1%) of the entomostracans. The dominance of *Diaptomus* and the sequence of *Cyclops, Limnocalanus* and Cladocera is maintained in all of the 7 years and the percentage which each genus contributes to the total Entomostraca does not vary greatly from year to year.

Among the rotifers, *Keratella* is most frequent, averaging 38%, *Kellicottia* follows with 26%. These two genera are quite consistent in their numbers throughout the 7 years. *Synchaeta*, which ranks third, with 15%, and *Asplanchna* and *Polyarthra*, which follow in that order, show considerable irregularity in their abundance from year to year. Thus in 1946 *Synchaeta* outnumbered *Keratella* and *Kellicottia* while in 1952 and 1953 *Asplanchna* became the most abundant genus of the rotifers.

The phytoplankters are completely dominated by *Melosira* which averages 74% of the phytoplankton and ranges from 55% in 1952 to 89% in 1954. *Asterionella* is second with an average of 15% and ranges from 7.4 to 26%. *Fragilaria* and *Tabellaria* follow in that order but rarely amount to as much as 5% of the algae. A single blue-green, *Anabaena*, was present in numbers sufficient for counting and then only in small numbers, averaging less than 1%. The chrysophycean, *Dinobryon*, was numerous in 1946 and again in 1952, but averaged less than 5% through the 7 years.

From the above data the plankton of Great Slave Lake can be characterized as a copepod-diatom population, or perhaps as a *Diaptomus-Melosira* community, but keeping in mind the volume dominance of *Limnocalanus*. The rotifers *Keratella* and *Kellicottia* are constant and characteristic genera but they too contribute only a small fraction of the volume of the net plankton.

In order to follow the seasonal variations in numbers of the different plankters through the 7 years it was necessary to examine the counts which are recorded in Tables C to I (Appendix). As a first stage of analysis, the values for total Entomostraca were plotted in Fig. 13, total rotifers in Fig. 14 and total phytoplankters in Fig. 15. From the curves showing the numbers of Entomostraca in each of the 7 years (Fig. 13), the averages have been computed at 5-day intervals and the resulting curve, showing the trend in numbers for 7 years, has been added as a bold line. This was done also for the rotifers and phytoplankters and the three curves showing 7-year averages have been plotted in Fig. 16. The Entomostraca are present in June and most of July in numbers between 8,000 and 11,000 per total vertical haul. They then decline at mid-August to below 5,000 but remain above 4,000 in the remainder of August and September. The rotifers, on the other hand, begin the season in small numbers and increase gradually to about 3,000 at August 5. This increase is continued with minor fluctuations to an average level of 8,000 in mid-September (Fig. 16) while in some years they reached 10,000 to 15,000 (Fig. 14). At the end of June the phytoplankters usually number 10 to 12 million cells per haul. This is followed by a rapid increase in the first half of July which in 1954 went well beyond 100 million cells per haul (Fig. 15). Toward the end of July a tremendous decrease

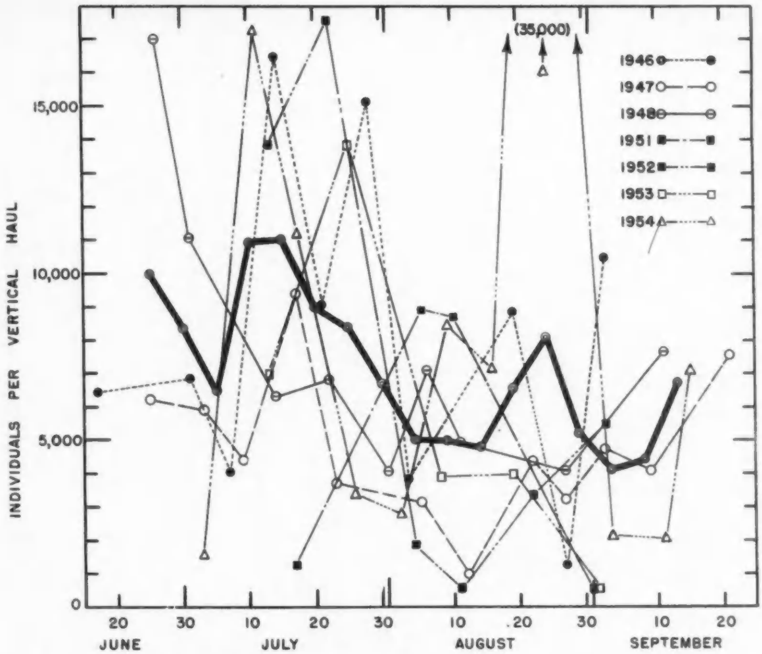

FIG. 13.—Numbers of Entomostraca through seven summers, also average for the 7-year period, at Station 31, Great Slave Lake. Note that the number per total vertical haul can be converted to the number per square metre by multiplying by 55.

takes place and by August 5 the average is down to 4 million (Fig. 16). From this point they increase again and vary between 4 and 7 million cells per haul to the end of the season. Thus the general trend in the numbers of algae tends to resemble that of the Entomostraca but the midsummer decrease is more violent in the former.

The seasonal sequence in numbers of nauplii, *Diaptomus, Cyclops* and *Limnocalanus* for each of the 7 years has been plotted on graphs similar to those in Fig. 13 to 15 and the average calculated in the same way. In the interest of brevity these four graphs have not been reproduced, but the 7-year average or "trend" curves have been assembled in Fig. 17. The nauplii are abundant early in the season, building up from 4,000 to 7,000 by mid-July. The decrease which follows is rapid until August 5 then slower to the end of the season. The *Diaptomus* population averages about 1,000 per haul until mid-July, then increases sharply to nearly 5,000 while the nauplii undergo their extensive decline. This would suggest that most of the nauplii in the early season period of abundance were those of *Diaptomus*. The numbers of *Diaptomus* usually increased from about 2,000 in early August to 4,000 at the end of the season. Figure 17 shows a second maximum of 5,000 in late August but this is due to

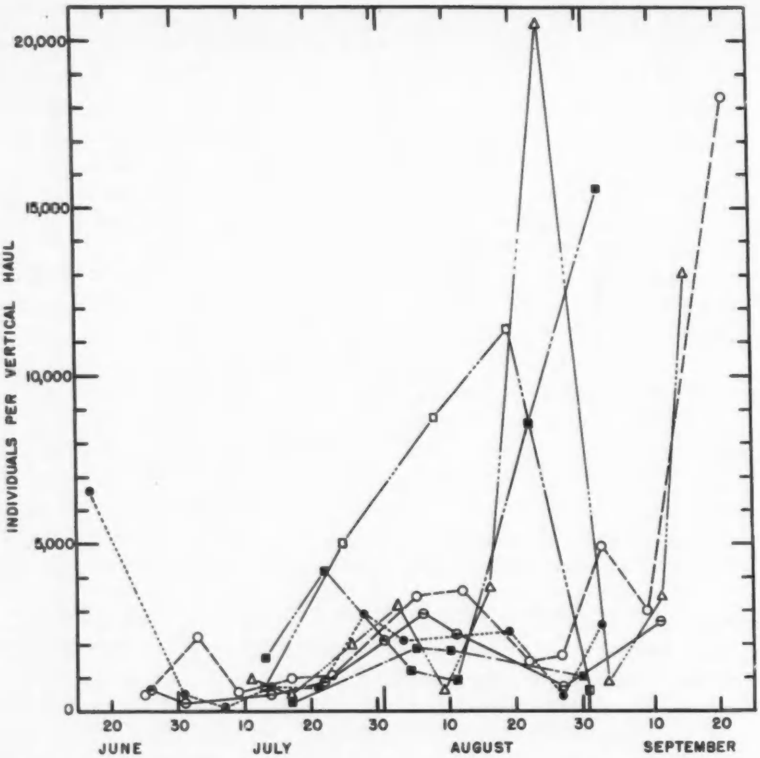

FIG. 14.—Numbers of rotifers through seven summers at Station 31, Great Slave Lake. Symbols as in Fig. 13.

the extraordinary occurrence of 23,600 *Diaptomus* in the haul of August 24, 1954 (Table I, Appendix). No such increase in numbers was observed in any of the remaining 6 years. The chief remaining genera of Entomostraca are subject to much less seasonal variation in their numbers, Fig. 17. *Cyclops* averages about 750 and shows brief periods of greater abundance about July 10 and August 25. The *Limnocalanus* population, averaging about 375 per haul, is amazingly steady, with a very gradual decline from about 500 early in the season to 150 in mid-September. The Cladocera made up less than 1% of the Entomostraca and were thus not present in sufficient numbers to warrant the preparation of graphs.

The 7-year trends in abundance of the five main rotifers in hauls at Station 31 are shown in Fig. 18. In a general way the sequence is one of small numbers in June and early July, steady increase through most of August, often followed by a slight decrease before the final upsurge to a maximum in mid-September which may be three or four times the average for the rest of the summer. *Synchaeta* appears to diverge from this pattern in having an extra maximum in late June.

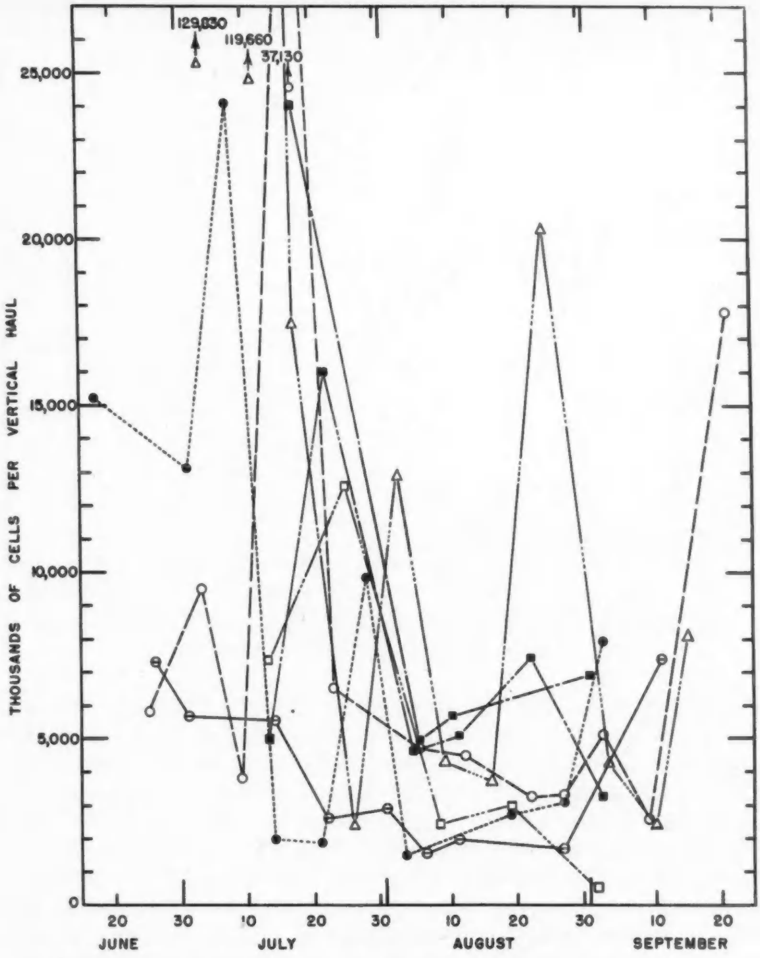

FIG. 15.—Numbers of phytoplankter cells through seven summers at Station 31, Great Slave Lake. Symbols as in Fig. 13.

This is due to unusual abundance in a single year 1946, when on June 17 there were 6,360 *Synchaeta* in a haul at Station 31 (Table C Appendix).

The average seasonal sequence in numbers of the major phytoplankters is indicated in Fig. 19. Numbers of the dominant genus *Melosira* show an early summer maximum, the great decline in late July and a relatively steady population of about 25 million cells per haul in August and September. However, in three of the seven years, 1946, 1947 and 1954, sudden pulses of *Melosira* went far beyond the ordinary maximum of about 10 million cells. The greatest pulse was

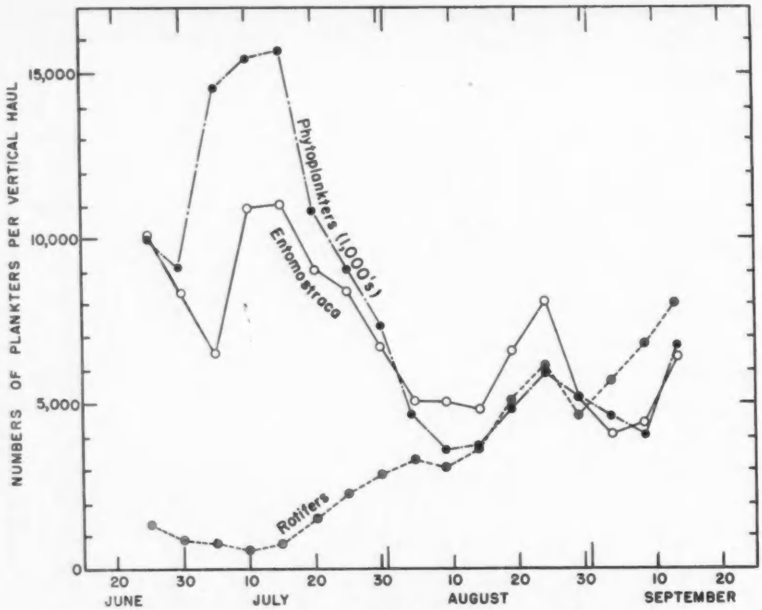

FIG. 16.—Seven-year average numbers of phytoplankter cells, Entomostraca and rotifers throughout the summer at Station 31, Great Slave Lake.

on July 3, 1954, when the *Melosira* count was 129.5 million cells. *Asterionella*, on the other hand, tends to increase gradually through most of the season averaging about 1.5 million cells and showing a sudden burst to about 5 million at mid-August. *Dinobryon*, from small beginnings in June tended to reach a maximum in the latter half of July. Marked pulses appeared on July 28, 1946 and July 22, 1952. After a midsummer decrease, a second maximum occurred about August 25. This was observed in 1946, 1951 and especially in 1954. Two other diatoms *Fragilaria* and *Tabellaria* might have been included in Fig. 19 but they contribute a very small percentage of the phytoplankton population. Both genera tend to be scarce until midsummer and then increase slowly toward a minor maximum in September. In 1953, *Fragilaria* showed an additional peak on July 13.

The foregoing analyses of the numerical composition of the plankton of Great Slave Lake has been based on the many collections made at Station 31 off Gros Cap in the years 1946 to 1954. We should now examine the numerical data on the plankton from other parts of the main lake to see whether Station 31 is, in fact, typical of the open lake and to find in what ways the plankton of various areas differs from that of the open water. These observations have been grouped in four tables, J to M (Appendix), representing more or less distinct parts of the lake. The stations in some of these areas vary considerably in depth,

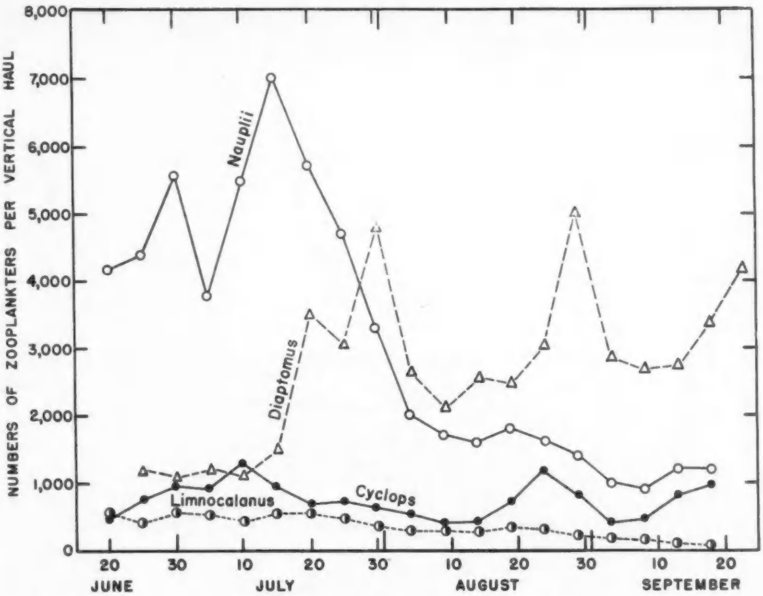

FIG. 17.—Seven-year average numbers of the dominant zooplankters at Station 31, Great Slave Lake.

and the dates of sampling are not in all cases representative of the whole summer. Nevertheless, it was found useful to calculate average numbers and percentage compositions for some of these areas to provide a basis for comparison.

The counts for eight stations in the open lake, Table J, show a marked similarity to those for the central Station 31, as recorded in Tables C to I and summarized in Table VI on page 95. The average numbers of the three major groups of organisms per vertical haul are as follows:

	Av. at Sta. 31	Av. for eight stations in open lake
Entomostraca	6,792	6,499
Rotifera	3,305	1,475
Phytoplankters (cells)	10,322,000	10,688,000

The lower numbers of rotifers at the open lake stations may be accounted for by the large proportion of these samples taken in June, when rotifers are few in all parts of the lake. Comparison of the percentage of each group made up by each genus at Station 31 and the other eight stations shows a very close correspondence e.g. *Diaptomus* 47.3 and 43.3%, *Cyclops* 10.9 and 10.6% respectively. Thus the numerical data support the gravimetric results (p. 74 above) in suggesting that the plankton at Station 31 is reasonably representative of that of the open water in the main part of Great Slave Lake.

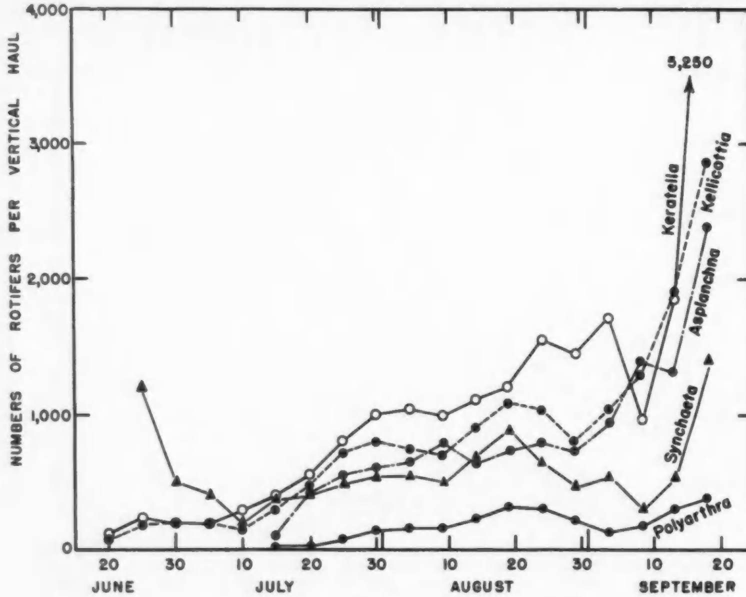

Fig. 18.—Seven-year average numbers of the dominant rotifers at Station 31, Great Slave Lake.

The plankton from a group of stations near Resolution and along the southwest shore is recorded in Table K. The plankton at these stations is light, the numbers of Entomostraca being about one-fifth, Rotifera one-half, and phytoplankters two-thirds that of the main lake. This is not surprising since the stations are all shallow, 11 to 30 metres, and since most of the samples in this area were taken too early in the season for much plankton development. It might also be thought that turbidity, resulting from the muddy inflow from the nearby Slave River delta, was a further adverse factor. This would seem to be contradicted by the observation that in the next group of stations which are also shallow but with mostly clear water, the phytoplankters are still less numerous.

The first four stations in Table L lie close to Outpost, a barren series of exposed rocky islands about 20 miles south of Gros Cap. Their plankton appears to be peculiarly scanty both in animal and plant forms. On the other hand there was an extremely rich plankton at Station 40 which is in the Inconnu Channel, about 30 miles east of Outpost. The last sample in Table L is from Station 8 near Redrock Point in the north arm. Here, on July 27, 1944, there was a plankton population above average in weight, unusually rich in rotifers and poor in phytoplankton. The counts for these varied stations have not been averaged since such a calculation would have little meaning.

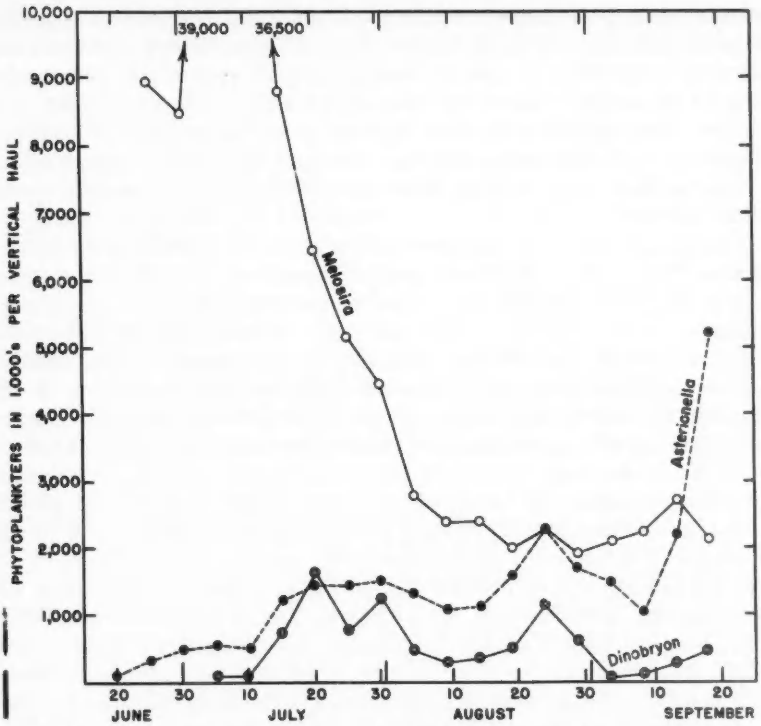

FIG. 19.—Seven-year average numbers of the dominant phytoplankters at Station 31, Great Slave Lake.

Yellowknife Bay is an area somewhat distinct from the main lake both in its physical limnology (Rawson, 1950) and in its bottom fauna (Rawson 1953a). In Table M there are recorded four samples from Station 5, in the deep, central part of the bay, and five from shallow stations mostly near Yellowknife. The average of the four deep samples is somewhat below that for the main lake with respect to Entomostraca, but considerably above the main lake average in rotifers and phytoplankters. When the very shallow stations are included, the average for Entomostraca is still lower but the other groups about equal those of the main lake. It is suspected that the greater warming of Yellowknife Bay may be related to the greater numbers of rotifers. A similar abundance of rotifers was observed in the warm waters of the Inconnu Channel.

PLANKTON OF THE EAST ARM

The plankton of the east arm was collected mainly in the years 1946 and 1947 and at two stations in Christie Bay. From a base at Pearson Point, collections

were made at Station 35, about 1 mile south and in 140 metres of water, and at Station 36, some 4 miles north in 600 metres of water. Numerical analyses of eight samples at Station 35 are recorded in Table N and of four samples from Station 36 in Table O. These analyses indicate the generic composition of the hauls and provide some indication of seasonal and annual differences in the plankton for the two summers. The remote location of Pearson Point, about 100 miles east of Gros Cap, made it difficult to obtain adequate samples in early and late summer.

Marked differences between the plankton of 1946 and 1947 are shown in the hauls from Station 35. In 1946 the Entomostraca were less than half as numerous as in 1947 but the phytoplankters in 1947 outnumbered those of 1946 by nearly five to one. Rotifers were about equally numerous in both years. The less extensive data from Station 36, Table O show a comparable situation for the phytoplankton, but here the Entomostraca of 1946 were slightly greater than those of 1947. While the sampling was not sufficiently frequent to follow seasonal changes in the plankton population, some trends can be observed. Thus Entomostraca tend to become less numerous from early July to late August, while rotifers, almost absent in July, appear in moderate numbers during August. Phytoplankters appeared to increase steadily during 1946, but in 1947 no obvious maxima were observed.

Additional samples of the plankton in the east arm of Great Slave Lake are recorded in Table P. Of particular interest are three counts from McLeod Bay, which, on the basis of mineral content, bottom organisms and fish population, has been found to be the most barren part of the lake. The average number of various plankters in these three samples appears in the fourth column of Table P. The average numbers in the major groups and the dry weights of the samples may be compared as follows:

	Station 31, main lake	Sta. 35 and 36, Christie Bay	Three stations, McLeod Bay
Entomostraca	6,792	2,467	1,395
Rotifera	3,305	122	101
Phytoplankters	10,322,000	45,720	185,885
Average dry weight in kg./ha.	23.7	14.3	9.0

The Entomostraca in the McLeod Bay samples are only a little more than half those of Christie Bay and the rotifers are also fewer in number. The phytoplankters, because of a pulse of *Melosira* and *Dinobryon* on August 13, 1945, are nearly four times the average for Christie Bay. This is not so impressive when it is noted that they are still less than one-fiftieth of the average number for the main lake. Thus the numerical data on the plankton bear out the earlier gravimetric evidence of low production in McLeod Bay.

Three miscellaneous samples from the east arm region are also recorded in Table P. Station 14 is in a shallow (28 metre) location near Snowdrift and about 8 miles south of Station 35. On the single date of sampling its Entomostraca were equal in numbers to the average at Station 35 (Table N) and the rotifers and phytoplankters were much more abundant. Station 42, in Wildbread Bay had

on August 21, 1946, a plankton crop which greatly exceeded anything observed in Christie Bay, with which it connects, and even approached the average for the main lake. The tremendous number of nauplii, a large number of rotifers and a pulse of *Dinobryon* were responsible for these numbers. It should be noted that although the numbers were high, the dry weight was only two-thirds of the average for the main lake. The last column in Table P is a record for Artillery Lake which lies some 25 miles east of McLeod Bay. Its location, partly in the barren lands, makes it of interest for comparison with Great Slave which lies in the wooded zone. The zooplankters were scanty in the single sample but the diatoms *Melosira* and *Asterionella* were abundant. It should be noted that *Limnocalanus* and *Bosmina* were present in the sample but not in sufficient numbers to appear in the count.

Comparing the composition of the plankton of the east arm with that of the main lake we find the same general dominance of copepods and diatoms. There are, however, interesting differences in the generic composition and in the relative amounts of phytoplankton. To facilitate this comparison Table VI has been

TABLE VI.—Comparison of average numerical and volumetric compositions of plankton hauls from the east arm and the main part of Great Slave Lake.

	Average of 12 hauls at Stations 35 and 36, Christie Bay 1946 and 1947			Average of 67 hauls at Station 31, main lake 1946 and 1954		
	Numbers	%	% Volume	Numbers	%	% Volume
Nauplii	1,733	70.2	1.9	3,219	47.3	0.9
Diaptomus	367	14.9	19.6	2,403	35.3	38.2
Cyclops	197	8.0	9.3	742	10.9	10.8
Limnocalanus	129	.5.3	55.0	374	5.5	48.7
Senecella	11	0.4	10.5	+	+	+
Epischura	4	0.2	0.3	+	+	+
Daphnia	25	1.0	3.5	34	0.5	1.3
Bosmina	1	+	+	20	0.3	0.1
Total Entomostraca	2,467			6,792		
Kellicottia	42	34.4	3.3	871	26.3	1.1
Keratella	15	12.3	0.9	1,250	37.8	1.1
Conochilus	50	41.0	3.3	+	+	+
Synchaeta	7	5.7	0.9	513	15.5	1.0
Asplanchna	7	5.7	91.5	473	14.3	96.5
Polyarthra	1	0.8	0.1	198	6.0	0.2
Total Rotifera	122			3,305		
Asterionella	27,267	59.6	18.0	1,597,000	15.5	4.3
Eunotia	1,471	3.2	0.4	+	+	+
Melosira	1,370	3.0	3.7	7,619,000	73.6	83.1
Tabellaria	3,791	8.3	48.8	165,000	1.6	8.4
Fragilaria	514	1.1	0.1	351,000	3.4	0.4
Stephanodiscus	25	0.1	1.3	+	+	+
Synedra	118	0.3	0.6	11,000	0.1	0.3
Dinobryon	10,576	23.1	17.0	486,000	4.7	3.1
Anabaena	466	1.0	+	93,000	0.9	0.4
Ceratium	120	0.3	10.0	+	+	+
Codonella	2	+	+	+	+	+
Total phytoplankters	45,720			10,322,000		
Ratio of phytoplankton volume to zooplankton volume		1 : 445			1 : 19	

prepared in which the average numbers of organisms in 12 hauls at Stations 35 and 36 in Christie Bay are compared with the averages of 67 hauls at Station 31 off Gros Cap in the central part of the lake.

In an earlier section it was indicated that the dry weight of plankton in the main lake was very much greater than that of the east arm. Looking now at Table VI the average number of Entomostraca in the main lake is 2.7 times, the rotifers 30 times, and the phytoplankters 200 times the numbers of these organisms in the plankton of the east arm. Among the Entomostraca of the east arm *Diaptomus* is still predominant, *Cyclops* and *Limnocalanus* occur in roughly similar proportions, but *Senecella,* the largest of the copepods, is common in the east arm and infrequent in the main lake. The cladocera, *Daphnia* and *Bosmina,* are few in both areas and the latter very scarce in east arm. The same six genera of rotifers are found in both areas but in the east arm *Conochilus* is abundant (41%) while in the main lake it made up less than 1% of the rotifer count.

The greatest contrast in the plankton of the two areas is found in the phytoplankters, those of the main lake being roughly 200 times as numerous as those of the east arm. Also, *Melosira,* which made up nearly 74% of the phytoplankton of the main lake, is present in only small numbers, 3%, in the east arm where *Asterionella* is now the dominant. *Dinobryon* contributes a much larger proportion to the plankton of the east arm than to that of the main lake, an observation of considerable interest since *Dinobryon* is widely regarded as an indicator of oligotrophy. A striking difference between the two areas is frequency of *Eunotia* which was rare in the main lake but common in the east arm, especially at the deep Stations in Christie Bay and in McLeod Bay. *Ceratium* and *Codonella* are actually much more common in the collections from the main lake, however on a percentage basis they are insignificant among the abundant phytoplankters of that area.

The vertical distribution of plankters at Stations 35 and 36 was investigated in 1946 and 1947 by taking a number of fractional vertical hauls with the large net and also by horizontal tows with the Clarke-Bumpus sampler. The fractional samples were centrifuged to determine the volume of plankton at each depth. These data have been discussed above, pages 74, 75 and 76, and the vertical distribution by volume was illustrated in Fig. 5. The results of numerical analysis of these materials are presented in Tables VII to X. Note in these tables, that the fractional units are not equal but are graded from a 10-metre unit at the surface to 100-metre units in the deepest water.

At Station 35 on July 17, 1947, the nauplii were rather uniformly distributed down to 100 metres and fewer below that depth (Table VII). *Diaptomus* and *Limnocalanus* show a slight concentration in the 0- to 10-metre stratum while *Cyclops* was greatly concentrated, with 65% in the upper 10 metres. On August 13 the nauplii and *Limnocalanus* were greatly concentrated near the surface while *Cyclops* had diminished in numbers and was more widely distributed. On July 17 the phytoplankters, chiefly *Asterionella* and *Fragilaria,* were more abundant in the 25- to 50-metre stratum than near the surface. On August 13, *Fragilaria* had

TABLE VII.—Depth distribution of plankters at Station 35, Christie Bay, July 17 and August 13, 1947.

ENTOMOSTRACA

Depth, *metres*	Nauplii	*Diaptomus*	*Limnocalanus*	*Cyclops*	*Senecella*	*Epischura*	*Daphnia*	Totals
July 17/47								
0–10	165	245	28	285	2	—	15	740
10–25	310	70	5	53	3	1	1	443
25–50	690	205	20	85	—	10	—	1,010
50–100	705	88	6	17	8	8	—	832
100–135	103	23	2	3	—	—	—	131
	1,973	631	61	443	13	19	16	3,156
Aug. 13/47								
0–10	280	20	300	30	—	—	21	651
10–25	145	5	35	40	—	—	—	225
25–50	49	7	39	6	—	—	1	102
50–100	50	35	35	15	2	1	—	138
100–135	43	13	27	16	—	—	1	100
	567	80	436	107	2	1	23	1,216

ROTIFERS AND PROTOZOA

	Kellicottia	*Keratella*	*Polyarthra*	*Conochilus*	*Ceratium*	*Codonella*	
July 17/47							
0-10	10	3	—	2	—	5	20
10–25	8	—	—	5	—	—	13
25–50	—	—	—	5	5	—	10
50–100	—	—	—	—	—	—	—
100–135	—	—	—	1	1	—	2
	18	3	—	13	6	5	45
Aug. 13/47							
0–10	80	20	10	—	110	—	220
10–25	5	10	—	—	25	5	45
25–50	3	1	—	—	1	—	5
50–100	10	—	—	—	5	6	21
100–135	9	8	—	—	12	5	34
	107	39	10	—	153	16	325

PHYTOPLANKTERS (cells)

	Asterionella	*Tabellaria*	*Stephanodiscus*	*Eunotia*	*Melosira*	*Fragilaria*	*Dinobryon*	
July 17/47								
0–10	1,000	—	—	10	—	250	—	1,260
10–25	3,120	—	—	—	—	—	—	3,120
25–50	3,400	50	—	100	250	1,250	30	5,080
50–100	1,120	50	—	295	75	50	—	1,590
100–135	120	—	4	93	45	—	—	262
	8,760	100	4	498	370	1,550	30	11,312
Aug. 13/47								
0–10	4,720	300	40	80	—	—	100	5,240
10–25	1,880	210	—	—	—	—	—	2,090
25–50	1,344	—	—	—	—	—	—	1,344
50–100	1,040	—	10	—	—	—	—	1,050
100–135	784	140	3	—	—	—	30	957
	9,768	650	53	80	—	—	130	10,681

practically disappeared and large quantities of *Asterionella* were found in the upper 10 metres.

Station 36, with a depth of approximately 600 metres, provided a special opportunity for the study of deep distribution of plankton organisms. In Table VIII the Entomostraca are shown to extend to the maximum depth in moderate

TABLE VIII.—Depth distribution of Entomostraca at Station 36, Christie Bay, on four occasions in 1946 and 1947.

Depth, *metres*	Nauplii	*Diaptomus*	*Limnocalanus*	*Cyclops*	*Senecella*	*Daphnia*	Misc.[a]	Totals
July 19, 1946								
0–10	897	208	87	103	6	10	4	1315
10–25	1043	167	29	47	14	2	1	1303
25–50	2109	153	33	53	5	—	—	2353
50–100	885	124	39	36	3	1	—	1088
100–200	222	8	12	12	2	—	—	256
200–300	99	9	9	—	1	—	—	118
300–400	13	5	6	—	4	—	1	29
400–500	15	12	16	4	—	—	—	47
500–600	46	31	23	60	1	—	—	161
Totals	5329	717	254	315	36	13	6	6670
Aug. 19, 1946								
0–10	2078	109	64	65	2	24	2	2344
10–25	682	83	68	27	3	4	10	877
25–50	50	35	53	5	6	—	2	151
50–100	14	21	31	3	1	—	—	70
100–200	7	4	3	2	—	1	—	17
200–300	10	3	3	—	—	—	1	17
300–400	6	3	3	1	1	—	—	14
400–500	3	1	1	—	—	—	—	5
500–600	11	3	2	2	—	1	—	19
Totals	2861	262	228	105	13	30	15	3514
July 18, 1947								
0–10	933	158	19	83	1	1	2	1197
10–25	679	66	7	24	5	—	—	781
25–50	687	68	9	46	6	—	—	816
50–100	323	61	11	37	2	—	—	434
100–200	48	1	3	3	—	—	1	56
200–300	11	4	1	2	—	—	—	18
300–400	14	5	1	3	1	—	1	25
400–500	7	5	2	4	—	—	—	18
500–600	5	18	1	9	2	—	2	37
Totals	2707	386	54	211	17	1	6	3382
Aug. 14, 1947								
0–10	2211	612	84	159	1	87	1	3155
10–25	39	41	8	14	—	3	1	106
25–50	49	78	29	16	3	—	1	176
50–100	2	12	7	—	3	—	2	26
100–200	8	4	2	1	4	—	—	19
200–300	13	3	1	—	3	1	—	21
300–400	22	9	3	7	2	—	—	43
400–500	10	5	2	5	—	—	—	22
500–600	12	5	2	6	—	21	—	46
Totals	2366	769	138	208	16	112	5	3614

[a]*Epischura, Bosmina, Holopedium, Leptodora*

numbers on two dates in 1946 and in 1947. The nauplii extend in large numbers to 100 metres in July of both years, while in August of both years they were heavily concentrated in the upper 10 metres. With only four observations this may be a temporary rather than a continued situation. *Limnocalanus* occurs in smaller numbers than *Diaptomus* or *Cyclops* but in rather constant numbers at all depths. *Cyclops* shows a definite tendency to concentration near the surface. *Senecella* was never concentrated near the surface and was commonly found in maximum numbers between 25 and 50 metres. See also Table IX. *Daphnia* was usually near the surface but on August 14, 1947, a number of specimens were taken in the 500- to 600-metre stratum. On each of the four dates the total Entomostraca from the deepest stratum was greater than that from either of those above it. This near-bottom concentration was particularly obvious on July 19, 1946, when the number of Entomostraca in the 500- to 600-metre haul was 161 while that in 400–500 was 47 and in 300–400 only 29. Similar features of the vertical distribution of Entomostraca are shown in Table IX which lists the catch of eight horizontal tows with the Clarke-Bumpus sampler at depths down to 300 metres. It was not possible with our equipment to tow this sampler at 600 metres to examine the apparent concentration of Entomostraca near the bottom.

TABLE IX.—Depth distribution of Entomostraca in Christie Bay as shown by eight horizontal tows of equal length with the Clarke-Bumpus sampler, July 15, 1947

Depth	Nauplii	*Diaptomus*	*Limnocalanus*	*Cyclops*	*Senecella*
metres					
Surface	5550	225	45	75	0
5	7300	880	210	660	5
10	7480	780	80	540	9
25	4140	770	150	255	15
50	1840	252	81	63	7
100	217	44	6	12	5
200	129	8	3	17	2
300	146	17	9	16	6

The distribution of phytoplankters in deep water is illustrated by Table X for Station 36 on July 16 and August 14, 1947. On these dates *Eunotia* and *Asterionella* were the most abundant phytoplankters while *Melosira*, so frequently dominant in the main lake, was third. The extensive depth distribution of these diatoms is of interest. Even in the clear water of Christie Bay, with 1% of the incident light reaching 10 or 12 metres, it would seem clear that there would be no light for photosynthesis in the deeper water e.g. 200 to 600 metres. Presumably the phytoplankters collected in these great depths are inactive or dead individuals sinking toward the bottom. It is possible, of course, that some of these individuals had adhered to the net from earlier hauls. This source of error was minimized by starting with a dry net and taking the fractional hauls in sequence from the bottom toward the surface. A second noteworthy feature of this table is the extreme paucity of phytoplankters even in the upper layers. Total vertical hauls of 5,922 individuals on July 18 and 3,826 on August 14 are equiva-

TABLE X.—Depth distribution of phytoplankter cells at Station 36, Great Slave Lake, July 16 and August 14, 1947.

	July 16						August 14					
Depth	*Eunotia*	*Asterionella*	*Melosira*	*Synedra*	Others	Total	*Eunotia*	*Asterionella*	*Melosira*	*Synedra*	Others	Total
metres												
0–10	1295	168	35	14	—	1512	384	448	20	4	9	865
10–25	224	112	105	—	—	441	152	1056	20	28	4	1260
25–50	273	128	140	—	—	541	40	652	8	8	20	728
50–100	535	—	165	—	9	709	81	96	—	6	50	233
100–200	84	80	70	—	1	235	4	48	—	2	—	54
200–300	78	128	140	—	—	346	3	48	45	3	—	99
300–400	98	224	370	—	72	764	51	144	30	3	20	248
400–500	7	512	370	7	106	1002	3	168	15	9	—	195
500–600	—	203	140	21	8	372	12	120	—	9	3	144
Total	2594	1555	1535	42	196	5922	730	2780	138	72	106	3826

lent to 300,000 and 200,000 phytoplankters per square metre. It is presumed that the microplankter forms which passed through the No. 20 silk net must be sufficient in number to compensate for this scarcity of larger algae.

NUMERICAL AND VOLUMETRIC ANALYSES

The common practice of expressing plankton composition only in terms of numbers of the component genera or species, is useful in a descriptive way but often misleading quantitatively. Thus in a given count of copepods, nauplii may outnumber *Limnocalanus* by 1000 to 1 but the average volume of a *Limnocalanus* may be 400 times that of a nauplius. Among the rotifers a single *Asplanchna* may be 200 times the volume of a *Keratella*. Under these circumstances the addition of numbers of various genera to arrive at a value for total Entomostraca or total Rotifera is somewhat absurd. The remedy would seem to be the calculation of average unit volumes for each species and expression of results both numerically and volumetrically. As an illustration, the 7-year average percentage volumes of organisms found at Station 31 have been inserted in Table VI along with the corresponding numbers and numerical percentages.

Looking first at the Entomostraca in Table VI, we find that at Station 31 *Diaptomus* and *Cyclops* contribute similar percentages both numerically and volumetrically. However the nauplii, which were nearly half the total number of Entomostraca, contribute less than 1% of the volume, while *Limnocalanus*, only 5.5% numerically, make up 48.7% of the volume. It would seem that *Limnocalanus* should be mentioned along with *Diaptomus* as dominant in the plankton of Great Slave Lake.

The five genera of rotifers at Station 31 contribute from 6 to 37.8% of the total number. *Asplanchna* contributes 14.3% of the number but its individuals are of such huge volume that it represents 96.5% of the total. Since the body of *Asplanchna* is sac-like and fluid filled, dry weight determination might provide a more reasonable basis for comparison. In any case it is difficult to consider *Asplanchna* as dominant over the much more numerous and constantly occurring *Keratella*.

The phytoplankters collected at Station 31 differ less widely in their magnitudes than do the zooplankters. Thus in Table VI the percentage volumes are not unlike the percentage by numbers. *Melosira* is distinctly dominant contributing 73.6% of the number and 83.1% of the volume.

Similar values for numerical and volumetric percentage of organisms found in Christie Bay are also given in Table VI. In this area the volumetric dominance of *Limnocalanus* is even greater than it was in the main lake and the other very large copepod, *Senecella*, also contributes 10.5% of the volume. Among the rotifers, *Asplanchna*, although less numerous than in the main lake, still contributes 91.5% of the volume. *Tabellaria*, whose individual cells are very much larger than those of *Asterionella* emerges as the bulkiest of the diatoms, 48.8%, while *Asterionella* volume is 18%.

A further application of the unit volume system is found in the calculation of volume ratios for the total phytoplankton and zooplankton. Such $p:z$ ratios

were calculated for the annual average plankton populations at Station 31 for the 7 years recorded in Table IV above. At this station the extremes run from 1:70 in 1948, a year of very low phytoplankton development, to 1:7 in 1954 when the phytoplankton was extremely heavy. The 7-year average $p{:}z$ ratio was 1:19.

A closer examination of the values in Table IV shows that during the 7 years Entomostraca varied from 67.5 to 97.8% in their contribution to the plankton volume. Rotifers were usually low, 0.8 to 3.2%, but in 1952 and 1953, because of unusual abundance of the very large rotifer *Asplanchna,* the percentages rose to 29.5 and 26.9%. Phytoplankters, although outnumbering the zooplankters by about 100 to 1, represented a much smaller fraction of the total volume ranging from 1.4 to 12.1%.

The relative scarcity of phytoplankters in the east arm as contrasted to the main lake is shown in Table VI by the extremely low average $p{:}z$ ratio of 1:445, to be compared with that of the main lake of 1:19. Ruttner (1940) found $p{:}z$ ratios as low as 1:15 in alpine lakes of Europe. Limnologists have long been surprised to find the volume of Entomostraca greatly exceeding that of the algae on which they depend for food. The discovery by Rodhe (1955) of large numbers of minute green algae, 1 to 2 microns or less in diameter and called by him "μ-algae", would seem to explain this apparent anomaly. It is unfortunate that the circumstances of our investigation did not allow us to investigate the nanno- or ultraplankton which passed through the No. 20 silk nets. Such information would have made possible the calculation of a true and more meaningful $p{:}z$ ratio for the total plankton.

DISCUSSION

The *composition* of the plankton of Great Slave Lake has been described in the foregoing sections. Qualitatively, it may be characterized as a diatom–copepod community, with the diatoms *Melosira* and *Asterionella* and the copepods *Diaptomus, Cyclops* and *Limnocalanus* as dominant genera. A more detailed examination of the phytoplankton reveals many species present but only a few of them occurring in any considerable numbers. In addition to the two diatoms listed as dominants, five genera, *Synedra, Tabellaria, Fragilaria, Stephanodiscus* and *Eunotia,* are of some importance. Few green algae except *Pediastrum* and *Staurastrum* are common in the open water. The chrysophycean *Dinobryon* and the dinophycean *Ceratium* are also important elements in the plankton. *Anabaena* is occasionally common but, as a group, the blue-greens are extremely scanty. It is noteworthy that the almost universal blue-green, *Microcystis,* is absent from our collections, however, small numbers of *Microcystis* were observed in Lake Athabaska which drains north into Great Slave Lake.

Of the three copepods mentioned as dominant, *Diaptomus* is the most numerous but *Limnocalanus* provides the greatest bulk. The other very large form, *Senecella,* was present in such small numbers as to render counting difficult, yet in the east arm it too provides an important fraction of the copepod volume.

Epischura was of erratic occurrence. Only two cladocerans, *Daphnia* and *Bosmina,* were sufficiently numerous for counting, but other well-known genera occurred in scattered locations. The rotifer population is dominated by *Keratella* in the main lake and *Kellicottia* in the east arm. *Synchaeta, Asplanchna, Polyarthra* and *Conochilus* are also common in the open water areas.

The volumetric composition has been worked out to supplement and correct the impressions given by numerical results. By this device *Limnocalanus* emerges as greater than *Diaptomus* and other genera fall into perspective (Table VI). Also, in Table IV, it is shown that *Entomostraca* contribute about 85.5% to the volume of plankton, rotifers 9.5%, and phytoplankters 5.0%, in the main lake. This indicates an average phytoplankton:zooplankton ratio of 1:19 for the main lake. In the east arm the phytoplankters are much less numerous and the p:z ratio becomes 1:445. Remembering that this is net plankton, it seems reasonable to assume that there must also be an extensive nanno- or ultraplankton on which the zooplankters are subsisting.

The *variability* in numbers and composition of the plankton has been examined both seasonally and annually. The average annual crop at a representative central station over a 9-year period showed a less than twofold variation (16.4 to 28.9 kg./ha.) and in most of the years the value was close to the mean of 23.7 kg./ha. Variation of the crop during the season was extensive but not without pattern. In each year there was evidence of an early summer maximum, a sharp decline in July and a second lesser maximum in late August and September. This sequence and the amount of divergence in the different years are shown for weight of plankton in Fig. 12 and for numbers of the three main groups of plankters in Fig. 13 to 15. The midsummer minimum, between early and late maxima is a pattern known in many areas. In Great Slave Lake the midsummer minimum is of short duration which would suggest a crowding together of the whole cycle into a relatively short ice-free season (6 1/2 months, Rawson 1950).

Combining the data from several years shows more clearly the seasonal trends, for groups (Fig. 16) and for genera (Fig. 17 to 19). With very few exceptions the maximum numbers for any group of plankters or for any genus does not exceed the seasonal average by more than four times. These exceptions include great pulses of *Melosira* in early July 1954 and tremendous numbers of Entomostraca on August 24 of the same year. This moderation in the extent of seasonal fluctuation is emphasized by the fact that it was not necessary to plot the graphs of seasonal abundance (Fig. 13 to 19) on logarithmic scales.

The identification of *ecological factors* responsible for conditions or changes in the plankton population is hardly to be expected in a descriptive study of this kind. Even an elementary approach to this problem would require determinations of such chemicals as nitrogen, phosphorus and potassium, in addition to the temperature, oxygen, pH and transparency which we were able to observe. Nevertheless, there has emerged a clear association of higher amounts of plankton with years of higher mean water temperatures. The average standing crop of plankton in five "warm" summers was 23.9 kg./ha. and for three "cold" summers 19.9 kg./ha. (page 80 above). The observations in the east arm were made

mostly in 1946 and 1947 and are not sufficiently numerous to allow calculation of the annual averages. However when the dry weights of the 24 samples from Christie and McLeod Bay (Table II) are compared with the temperatures at the 10-metre depth on the days of collection some evidence of positive correlation is obtained. In 13 cases where the temperature at 10 metres was between 2.4 and 6.4° C. the average plankton was 8.5 kg./ha. In 8 cases where the temperature at 10 metres was between 6.8 and 12.6° C. the average plankton was 24.4 kg./ha. Such a relation is barely detectable in the main lake, which would lead to the deduction that in the cold east arm, low water temperature is more important as a limiting factor for plankton production than in the main lake. The dominance of *Asterionella* in the east arm and *Melosira* in the main lake would also support this conclusion.

The adverse effect of turbidity on plankton production appears to be illustrated by events in the summer of 1948. In that season the plankton failed to reach the usual mid-July maximum although the temperatures rose steadily and the season would be classified as a "warm" year (Fig. 10). The inflow of muddy water from the Slave River occurred about July 10 and light penetration was low through the midsummer period (Fig. 11). A decline in the plankton crop early in September 1954 may also be attributed to increased turbidity, although high turbidity in August of that year was not associated with decreased plankton.

The presumed effect of morphometry, measured crudely by mean depth, on the standing crop of plankton in the main part of Great Slave, Christie Bay and McLeod Bay, has been referred to above, page 74. It was also pointed out that McLeod Bay, though only half as deep as Christie, had a lighter plankton population, possibly because of its much lower mineral content. Thus an edaphic influence may be added to temperature and turbidity as probable factors in control of the plankton crop of Great Slave Lake.

The extensive decline in the plankton during the latter part of July is a prominent feature both in the gravimetric and numerical data. In the absence of detailed chemical information, consideration of the reasons for this decline must be largely speculative. It is commonly suggested that the spring or early summer maximum of phytoplankton uses up some essential nutrients and then drops off sharply. This might well be followed by a decline in zooplankters dependent on the algae for food. In Great Slave Lake the decline in Entomostraca begins at the same time as that of the phytoplankters, Fig. 16. From Fig. 17 it will be seen that only the nauplii began to decrease on July 15 and that *Diaptomus*, the main item of the copepods, continued to increase until July 30. Thus the increase in *Diaptomus* coincided with that of decrease in phytoplankters on which they fed. It is conceivable that the reason for decrease in the Entomostraca might be heavy feeding by fish at this time. The low period for Entomostraca is August 1 to 15 and Kennedy (1953) has shown that in Great Slave Lake "almost one-half of the annual growth (of the whitefish *Coregonus clupeaformis*) takes place during the first half of August." It might be expected that the main plankton feeding-fish, *Leucichthys*, would also show a maximum of feeding and growth at this time.

The direct *utilization of plankton as food for fish* was discussed by the writer in an earlier paper (Rawson 1951b). The fish of Great Slave Lake are dominated by three species, the ciscoes, *Leucichthys* spp., the common whitefish, *Coregonus clupeaformis*, and the lake trout, *Cristivomer namaycush*. Adult ciscoes feed mainly on plankton as do also the young of many species in the lake. The ciscoes in turn, provide the major source of food for the lake trout. The whitefish eats little plankton except in its first year, but its main food is *Pontoporeia*. The crustaceans *Pontoporeia* and *Mysis*, feeding on plankton and on planktogenous detritus, provide appreciable amounts of food for five larger species of fish in the lake.

The feeding of ciscoes on plankton was shown (Rawson 1951b) to vary somewhat in different parts of the lake. In the east arm 88% of the volume of their food was of copepods, in Yellowknife Bay only 37% and for the whole lake an average of 60%. Most of the remaining food of ciscoes was *Mysis*, with minor quantities of insect larvae, Cladocera and *Gammarus*. In the extremely deep waters of McLeod and Christie Bays the bottom fauna is so scanty and remote as to be almost unavailable to the fish populations. Thus in these areas there exists a truly limnetic association with plankton, *Mysis*, ciscoes and lake trout in a food cycle relatively independent of the benthic community.

The *typology* of a lake is indicated both by the quantity and the composition of its plankton. With regard to quantity the plankton of Great Slave Lake has been shown to fit very closely into a series of large lakes where the productivity is believed to be controlled mainly by the morphometric situation (Rawson 1953b) and Fig. 6 above. Moreover the difference between the weight of plankton in the main lake and that in Christie and McLeod Bays are believed to indicate successive degrees of oligotrophy. The main lake plankton averaged 23.7 kg./ha., Christie Bay 14.3 and McLeod Bay 9.0 kg./ha. The latter certainly represents an extreme condition of oligotrophy. It may be noted here that three samples of plankton collected from Great Bear Lake by Dr. R. B. Miller and analysed by the writer in 1945, show an amount and quality very like that of Christie Bay.

The qualitative indications of oligotrophy in Great Slave Lake are by no means as clear-cut as the quantitative evidence presented above. From the long-continued and intensive studies of plankton in lakes, mainly of northern Europe, there has emerged a body of information on plankton types and species indicative of eutrophic and oligotrophic conditions. As Naumann (1931) points out, it is generally agreed that the plankton of oligotrophic lakes is dominated by the Chlorophyceae (often Desmids), Chrysophyceae such as *Dinobryon* and occasionally by the diatom genera *Cyclotella* and *Tabellaria*. Eutrophic plankton is characterized by abundance of diatoms such as *Synedra, Fragilaria, Asterionella* and *Melosira*, by the blue-green algae and sometimes by *Ceratium* and *Pediastrum*. Similar statements concerning the characteristic phytoplankton of eutrophic and oligotrophic types have been incorporated in the literature concerning North American lakes, by Prescott (1939), Welch (1952) and others. It is at once evident that several of the dominant diatom genera of Great Slave Lake

have been considered as eutrophic. They are in fact, dominant in such highly eutrophic American lakes as Mendota (Birge and Juday 1922). The phytoplankton of Great Slave Lake is dominated by *Melosira islandica* which is regarded by European workers as somewhat eutrophic. Also the plankton of Great Slave Lake is not rich in desmids which are considered to be characteristic of oligotrophic lakes. However, as Hutchinson (1941) indicates, desmids are abundant in oligotrophic lakes deficient in calcium and, while the water of Great Slave Lake is low in minerals generally, it is not deficient in calcium (Rawson 1950). *Dinobryon*, another indicator of oligotrophy, is common but rarely abundant in Great Slave Lake. It is significant however that *Dinobryon* is much more numerous in the extremely oligotrophic east arm than in the main lake. Jarnefelt (1952), in a recent intensive study of plankton species as indicators of trophic lake types, finds *Keratella quadrata* only in eutrophic lakes and records *Asplanchna priodonta* as occurring much more abundantly in eutrophic than in oligotrophic lakes in Finland. Both of these species are common in Great Slave Lake. In fact, the only strong point of agreement between the plankton of Great Slave Lake and the so-called oligotrophic plankton type is the great scarcity of blue-green algae. Since Great Slave Lake in all other respects shows a high degree of oligotrophy, we may assume that the plankton of our large oligotrophic lakes differs considerably from that of the oligotrophic lakes of Europe, an assumption amply born out by the following comparison of plankton in Great Slave and other large lakes in North America. It is suggested that existing concepts of phytoplankton indicators of oligotrophy are in need of revision.

A *comparison with plankton of other lakes* should include both quantitative and qualitative data. Unfortunately, because of lack of uniformity of the means of collection, analysis and the expression of results, there is relatively little *quantitative* data available for comparison of the amount of plankton of Great Slave with that of other large lakes in North America. A comparison of the dry weights of net plankton from lakes of northern and western Canada has been made in an earlier paper (Rawson 1953b) and in Fig. 6 above. There is however a considerable body of data for the *qualitative* comparison of the plankton of Great Slave Lake with that of Lake Winnipeg, Lake Nipigon and the Great Lakes. Some of the essential features for such a comparison are drawn together in Table XI, where the dominant forms of each plankton group, as indicated by various authors, are listed for seven lakes.

Considering first the phytoplankton it is evident that in all these lakes the diatoms are dominant, usually forming more than 80% of the total numbers. *Melosira granulata* leads in Nipigon, Superior and Ontario, and is reported from Winnipeg, Superior, Michigan and Erie. The *Melosira* of Great Slave Lake is *M. islandica* and Ahlstrom (1936) reports this species as dominant in Lake Michigan. *Asterionella formosa* leads in the remaining lakes. *Tabellaria fenestrata, Fragilaria crotonensis, Synedra* sp. and *Stephanodiscus* sp. are present in all of the lakes, usually in considerable quantities. The Chlorophyceae are not abundant in the open waters of these large lakes. Those which do occur are usually of the genera *Dictyosphaerium* and *Scenedesmus*. In the two relatively shallow members

TABLE XI.—Summary of the dominant plankters in the open waters of Great Slave Lake, Lake Winnipeg, Lake Nipigon and the Great Lakes, from various authors. Where information is available the genera in each group are listed in order of abundance.

Dominant plankters / Chief sources of information	Great Slave Lake	Lake Winnipeg	Lake Nipigon	Lake Superior	Lake Michigan	Lake Erie	Lake Ontario
	This study	Bajkov (1930) Lowe (1924)	MacKay (1951) Bigelow (1923) " (1928)	Eddy (1934) Eddy (1943) Taylor (1935)	Ahlstrom (1936) Damann (1938) Eddy (1927)	Chandler (1940) Chandler & Weeks (1945)	Tucker (1948) Pritchard (1931)
Phytoplankters							
Diatomaceae	*Melosira* *Asterionella* *Tabellaria* *Fragilaria* *Synedra* *Stephanodiscus*	*Asterionella* *Stephanodiscus* *Tabellaria* *Fragilaria* *Melosira*	*Melosira* *Asterionella* *Tabellaria* *Synedra* *Stephanodiscus* *Fragilaria*	*Melosira* *Fragilaria* *Asterionella* *Tabellaria*	*Asterionella* *Synedra* *Fragilaria* *Tabellaria* *Melosira* *Cyclotella*	*Asterionella* *Synedra* *Tabellaria* *Fragilaria* *Melosira* *Stephanodiscus*	*Melosira* *Tabellaria* *Fragilaria*
Chlorophyceae	*Staurastrum* *Pediastrum* Not abundant	*Dictyosphaerium* *Scenedesmus* Not abundant	"rare in open water"	*Pediastrum* (scarce)	*Closterium* *Sphaerocystis* *Dictyosphaerium* (all scarce)	*Dictyosphaerium* *Scenedesmus* *Pediastrum* abundant July, Aug.	*Mougeotia* *Coelosphaerium* *Scenedesmus*
Chrysophyceae	*Dinobryon*	*Dinobryon*	*Dinobryon* common in bays only	*Dinobryon* (abundant)	*Dinobryon* spp. (abundant)	*Dinobryon* (not abundant)	*Dinobryon* (small numbers)
Myxophyceae	*Anabaena* (infrequent)	*Anabaena* and *Aphanizomenon* (abundant only at south end)	*Microcystis* *Anabaena* *Aphanizomenon* (scanty)	"almost absent"	*Oscillatoria* *Microcystis* *Anabaena*	*Aphanizomenon* *Merismopedia* *Microcystis* abundant July, Aug.	*Aphanizomenon* *Microcystis* Aug. and Sept.
Zooplankters							
Rotifera	*Keratella* *Kellicottia* *Synchaeta* *Asplanchna* *Polyarthra* *Conochilus*	*Keratella* *Kellicottia* *Polyarthra*	*Keratella* *Kellicottia* *Polyarthra* *Synchaeta* *Ploesoma*	*Keratella* *Kellicottia* *Polyarthra* *Asplanchna*	*Keratella* *Synchaeta* *Kellicottia* *Gastropus* *Polyarthra* *Asplanchna*	*Keratella* *Polyarthra* *Kellicottia* *Asplanchna* *Synchaeta*	*Keratella*
Copepoda	*Diaptomus* *Cyclops* *Limnocalanus* *Senecella*[a] *Epischura*	*Diaptomus* *Epischura* *Cyclops* *Limnocalanus*	*Diaptomus* *Cylops* *Limnocalanus* *Epischura* *Senecella*	*Diaptomus* *Cyclops* *Limnocalanus* *Epischura* *Senecella*	*Diaptomus* *Cyclops* *Epischura* *Limnocalanus*	*Cyclops* *Diaptomus* *Epischura* *Limnocalanus* (few)	*Cyclops* *Diaptomus* *Epischura* *Limnocalanus* *Senecella*
Cladocera	*Daphnia* *Bosmina*	*Daphnia* *Leptodora* *Bosmina*	*Daphnia* *Leptodora*	*Daphnia* *Bosmina*	*Bosmina* *Daphnia*	*Bosmina* *Daphnia* not abundant	*Daphnia*
Protozoa	*Ceratium* *Codonella*	*Ceratium*	*Difflugia*	*Ceratium* *Codonella* *Difflugia*	*Ceratium* *Codonella* *Difflugia*	*Ceratium* *Codonella* *Difflugia*	*Ceratium* *Peridinium* (few)

[a]*Senecella* should be considered as a characteristic, rather than a dominant, form in these lakes.

of the series, Winnipeg and Erie, green algae are more frequent and in the latter, Chandler (1940) reports them as making up 40% of the phytoplankton during the summer months. The Chrysophyceaean, *Dinobryon*, mainly *D. divergens*, is common in all the lakes but usually contributes only a small percentage of the population. Ahlstrom (1936) refers to Lake Michigan as a "*Dinobryon* lake" but he and Damann (1938) indicate the dominance of diatoms in this lake. Blue-green algae are rarely numerous in any of these lakes although *Anabaena* spp. and *Aphanizomenon* are frequently present. Again the partial exceptions are for the shallower and warmer lakes, Erie and Winnipeg where at midsummer, some blooming is observed. Bajkov, 1930, noted the greater abundance of blue-greens in the shallow southern portion of Lake Winnipeg.

The characteristic zooplankters of these lakes are copepods and rotifers, with a number of Cladocera present but rarely abundant. *Mysis relicta* is, of course, found in all of these lakes. *Keratella cochlearis* dominates the rotifers in almost every lake of the series and *Kellicottia* (formerly *Notholca*) *longispina* is frequently second. Other relatively constant species are *Synchaeta stylata, Polyarthra* sp. and *Asplanchna priodonta*. Among the copepods *Diaptomus* spp., *Cyclops, Epischura lacustris, Limnocalanus macrurus* and *Senecella calanoides* are the characteristic forms. Several species of both *Diaptomus* and *Cyclops* are common in these lakes and specific information as to dominance is scanty. *Diaptomus minutus, D. tenuicaudatus* and *D. ashlandi* are among the more widespread species (*D. sicilis* is now considered inseparable from *D. tenuicaudatus*). *Cyclops bicuspidatus* would seem to be the most abundant of this genus. *Limnocalanus* is common in each of the eight lakes and *Senecella* probably occurs in all except the more shallow, Winnipeg and Erie. Among the Cladocera, *Daphnia longispina* and *Bosmina longirostris* appear to be the most constant although the *Bosmina* recorded from Great Slave Lake is *B. obtusirostris*.

Three samples of plankton from Great Bear Lake sent to the writer in 1945 by Dr. R. B. Miller of the University of Alberta, showed the same dominant forms. *Asterionella* was the chief diatom, *Dinobryon* was present, *Keratella* and *Kellicottia* were the main rotifers. *Diaptomus*, *Cyclops* and *Limnocalanus* were the abundant copepods which made up the large part of a very thin plankton. The writer has also had occasion to examine the plankton of Athabaska (Rawson, 1947), and Lac la Ronge (Rawson and Atton, 1953), lakes lying in Saskatchewan and between Great Slave Lake and Lake Winnipeg. In almost every respect both phyto- and zooplankton of these Saskatchewan lakes resembles in composition, that of others in the series listed in Table XI.

In view of the constancy of the above-mentioned species of plankters in the lakes under discussion and since these lakes are undoubtedly oligotrophic, it would seem reasonable to consider these species as characteristic of oligotrophy in large lakes. This does not imply that the presence of these species will serve to distinguish oligotrophic from eutrophic lakes for, as is well known, most of them are found in both types. It was indicated above that this finding disagrees in many respects with the lists of indicator species observed in European lakes and often quoted in American papers. It may be added that, in the writer's

experience, the plankton of small oligotrophic lakes in western Canada also fails to fit the European scheme; e.g. their phytoplankton is dominated by *Melosira* and *Asterionella* rather than by desmids or *Dinobryon*.

SUMMARY AND CONCLUSIONS

1. An annotated list of the net plankters from Great Slave Lake includes 160 Algae, 7 Protozoa, 26 Rotifera, 13 Copepoda and 11 Cladocera. These were collected mainly from the open water, with little attention to the inshore environment.

2. The diatoms dominate the phytoplankton with *Melosira islandica* and *Asterionella formosa* leading and *Tabellaria fenestrata, Fragilaria crotonensis, Synedra ulna* and *Stephanodiscus niagarae* also abundant. The green algae are insignificant in numbers but frequently represented by *Pediastrum boryanum* and *Staurastrum* spp. The chrysophycean, *Dinobryon divergens*, is common and occasionally abundant and the dinophycean, *Ceratium hirundinella*, is common.

3. The copepods dominate the zooplankton and, in volume, far exceed all other forms including the phytoplankton. *Diaptomus minutus* and *tenuicaudatus, Cyclops bicuspidatus, Limnocalanus macrurus, Epischura lacustris* and *Senecella calanoides* are the characteristic species. The cladocerans *Daphnia longispina* and *Bosmina obtusirostris* are present in small numbers. The rotifers contribute a small, but relatively constant, portion of the plankton with *Keratella cochlearis* and *Kellicottia longispina* dominant.

4. The net plankton of the deeper and more oligotrophic east arm differs from that of the main lake in having much fewer phytoplankters, *Asterionella* more abundant than *Melisira, Dinobyron* relatively more numerous and *Eunotia* present in considerable numbers. *Conochilus* is the most abundant rotifer and *Senecella calanoides* is more frequent than in the main lake.

5. The copepods contribute about 85% of the net plankton volume, rotifers 10% and phytoplankters only 5%. The average phytoplankton : zooplankton ratio in the main lake is about 1:19 but in the east arm only 1:445, Tables V and VI.

6. The average dry weight of the net plankton in the main lake over a period of seven years was 21.8 kg./ha. This is a light standing crop, about one-eighth that of the net plankton in the eutrophic lake, Mendota. The average for Christie Bay was 14.3 kg./ha. and for McLeod Bay 9.0 kg./ha. These values are in harmony with the observed inverse relation between mean depth and standing crop of net plankton in large lakes as described by the writer (Rawson 1953b).

7. Seasonal changes in the plankton of Great Slave Lake usually include a great increase in the diatoms and copepods beginning after the break-up of the ice in early June, reaching a maximum in mid-July then declining rapidly to a minimum in early August. The late summer increase reaches a lower maximum than that in July and it includes a great increase in the number of rotifers (Fig. 16). The amplitude of seasonal variation in numbers of plankters was less than that commonly observed in other lakes. The maxima in various groups rarely

exceeded the seasonal average by more than four times. Once, in July 1954, the numbers of *Melosira* increased to about 17 times the 7-year average.

8. Annual differences in the average dry weight of the plankton were usually small, but in 1950 dropped to 70% and in 1954 rose to 120%, of the 9-year average. Annual differences in the species composition of the plankton were not extensive and rarely changed the order of dominance among the main organisms. Minor exceptions to this statement are the rotifers *Synchaeta* and *Asplanchna* and the chrysophycean *Dinobryon* each of which was "abnormally" abundant in two or more years, Table V.

9. Annual differences in the standing crop of plankton were related mainly to water temperatures, the average crop in five "warm" summers exceeding that of the average in three "cold" summers by 20%. Seasonal decreases in the amount of plankton were on two occasions clearly related to increased turbidity. The lower plankton crop of McLeod Bay as compared to that of the still deeper Christie Bay is interpreted as an edaphic effect, since McLeod has only one-fifth as much mineral content as Christie.

10. From 50 to 70% of the plankton in a given area was usually found in the upper 25 metres. A further amount of 15 to 20% was between 25 and 50 metres and from 7 to 20% between 50 and 100 metres. The plankton below 100 metres rarely exceeded 10% of the total. Copepods were found in moderate numbers down to 600 metres, (Tables VIII and IX).

11. The moderate quantity and thin distribution of plankton in Great Slave Lake agrees with its obviously oligotrophic character. However the species composition of the plankton does not fit the usually accepted description for oligotrophic plankton and several of its dominant species are commonly considered as eutrophic indicators. It is clear that the description of oligotrophic plankton, drawn mainly from smaller lakes of northern Europe, does not apply to Great Slave nor the other very large lakes in North America.

12. A comparison of the plankton species found in Great Slave Lake with those of Lakes Winnipeg, Nipigon and the Great Lakes, reveals a remarkable similarity in their major species. All have a diatom–copepod type of plankton including the dominant species listed in 1 and 2 above and others in Table XI.

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APPENDIX

Table A.—Temperature and light penetration at Station 31, off Gros Cap, 1946 to 1948.

1946	June 17	June 23	June 30	July 7	July 14	July 21	July 28	Aug. 3	Aug. 19	Aug. 27	Sept. 2
					Temperature, °C.						
Air	7.6	6.6	9.0	12.0	9.0	15.5	16.2	17.9	18.0	15.0	17.0
Surf.	2.0	2.5	4.0	4.9	9.6	10.5	10.8	13.2	14.6	8.6	11.3
5 *m.*	—	—	—	—	5.2	9.0	10.2	9.5	—	6.3	—
10 *m.*	1.9	2.4	3.9	4.3	4.8	7.9	9.4	8.0	10.5	5.7	11.1
15 *m.*	—	—	—	—	—	5.3	7.6	6.8	—	—	—
25 *m.*	1.9	2.3	3.8	—	4.2	—	6.2	6.8	8.3	—	11.4
50 *m.*	1.2	2.4	3.6	3.6	4.0	5.1	4.9	4.4	6.0	4.5	8.5
140 *m.*	2.1	2.7	3.4	3.6	3.8	4.2	4.8	4.8	4.7	4.4	4.8
					Secchi disc, *metres*						
	5.0	5.3	5.5	—	7.3	4.5	3.5	3.8	5.0	3.5	3.6

1947	June 25	July 3	July 9	July 16	July 23	July 29	Aug. 5	Aug. 12	Aug. 22	Aug. 27	Sept. 2	Sept. 9	Sept. 21
						Temperature, °C.							
Air	4.1	9.8	8.5	10.0	10.3	—	—	9.8	9.0	11.5	12.0	12.5	0.0
Surf.	2.2	4.0	3.5	5.8	8.5	9.4	8.8	8.2	10.0	10.5	10.7	9.5	6.9
5 *m.*	—	—	—	—	5.7	9.3	8.6	7.6	—	10.1	10.4	—	—
10 *m.*	2.1	3.9	3.3	—	5.3	9.0	5.2	5.3	—	9.4	10.2	—	—
15 *m.*	—	—	—	—	5.0	7.3	4.4	5.1	—	8.2	8.9	—	—
25 *m.*	2.0	3.9	3.2	5.2	4.6	4.9	4.1	4.8	7.7	6.2	6.8	9.1	7.1
35 *m.*	—	—	—	—	4.4	4.6	4.0	4.0	—	5.3	5.4	—	—
50 *m.*	2.6	4.3	3.4	4.9	4.3	4.4	3.9	4.0	5.3	4.8	5.0	8.6	4.5
140 *m.*	3.8	4.6	3.2	4.9	4.3	—	3.9	3.7	4.0	4.1	4.3	4.5	4.1
						Secchi disc, *metres*							
	—	7.4	4.9	8.0	5.0	—	3.2	2.2	3.5	4.0	5.0	3.5	2.0

1948	June 25	July 1	July 8	July 14	July 22	July 31	Aug. 6	Aug. 11	Aug. 26	Sept. 11	Sept. 13
					Temperature, °C.						
Air	8.2	8.0	12.2	16.2	19.0	11.0	18.0	20.2	9.5	1.4	—
Surf.	3.8	3.9	7.8	14.0	16.0	10.3	14.5	18.3	9.8	8.9	9.5
5 *m.*	—	—	5.3	8.6	15.4	8.2	12.7	14.1	9.6	8.8	9.4
10 *m.*	3.8	3.9	4.9	6.7	13.0	7.0	11.5	11.4	9.4	8.7	9.2
15 *m.*	—	—	4.5	5.5	6.7	5.5	10.3	11.0	8.7	8.6	8.8
25 *m.*	3.8	3.9	4.3	4.3	4.9	4.9	8.0	8.7	8.0	8.5	7.9
50 *m.*	3.8	4.2	4.1	4.2	4.2	4.6	3.9	5.5	7.7	6.7	6.7
100 *m.*	3.9	4.2	4.2	3.9	4.5	4.2	3.9	4.6	5.0	5.0	5.0
140 *m.*	—	4.1	3.6	3.6	4.2	3.9	3.9	4.2	4.2	4.7	—
					Secchi disc, *metres*						
	4.5	6.5	4.5	1.3	0.7	1.3	0.5	1.0	2.0	2.0	—

TABLE B.—Temperature and light penetration at Station 31, off Gros Cap, 1949 to 1954.

	1949					1950				1951				1952					
	June 21	July 11	July 25	July 27	Aug. 11	July 4	July 21	Aug. 10	Aug. 23	July 16	Aug. 6	Aug. 10	Aug. 31	July 13	July 22	Aug. 4	Aug. 12	Aug. 22	Sept. 1
	Temperature, °C.																		
Air	15.5	13.5	13.5	—	17.5	25.0	18.3	15.5	12.8	13.0	20.0	15.0	19.0	—	20.0	14.0	13.9	11.1	12.3
Surf.	7.0	10.0	9.0	9.5	13.5	2.8	7.0	10.0	7.0	7.4	16.5	16.5	14.1	13.4	14.3	13.2	9.7	11.6	10.6
5 *m.*	—	9.0	8.5	9.0	13.0	2.8	5.0	9.0	6.8	6.0	12.3	15.4	13.9	9.8	11.0	11.2	9.5	11.5	10.1
10 *m.*	—	5.2	7.8	7.5	12.0	2.9	4.2	8.5	6.7	5.4	11.2	14.4	13.8	7.0	9.5	10.5	9.2	11.3	10.0
15 *m.*	—	5.0	7.8	7.2	11.2	2.9	3.9	7.0	6.5	5.2	9.0	12.7	13.3	6.2	9.4	10.2	8.7	10.0	8.1
25 *m.*	3.2	4.5	7.5	6.5	9.8	3.0	3.9	5.8	6.1	4.9	6.6	9.4	9.8	5.2	7.1	6.0	6.2	6.5	6.4
50 *m.*	—	3.8	6.7	5.8	8.5	3.1	3.9	4.3	4.6	4.8	5.4	6.0	5.8	4.1	5.8	5.3	5.7	6.4	6.3
75 *m.*	—	3.7	6.0	5.4	5.6	3.1	3.9	4.0	4.4	4.7	5.2	5.7	5.3	3.9	5.3	5.3	4.9	5.2	5.1
100 *m.*	—	3.6	5.0	4.9	5.1	3.1	3.9	4.0	4.0	4.2	5.0	5.4	5.0	3.8	5.2	4.5	4.7	4.8	4.7
140 *m.*	3.0	3.5	3.9	4.3	4.1	3.1	3.9	3.9	4.0	4.2	4.9	5.2	4.9	3.8	5.1	4.5	4.4	4.5	4.4
	Secchi disc, *metres*																		
	5.5	3.5	4.5	—	2.8	4.6	7.6	7.6	4.9	4.0	2.0	0.8	3.5	4.5	2.8	2.7	3.8	4.1	4.5

	1953					1954										
	July 13	July 25	Aug. 8	Aug. 19	Sept. 1	July 3	July 11	July 17	July 26	Aug. 2	Aug. 9	Aug. 16	Aug. 24	Sept. 3	Sept. 11	Sept. 15
	Temperature, °C.															
Air	15.0	18.0	19.0	16.0	14.0	25	12	12	—	14	19	17	12	12	16	—
Surf.	4.1	11.0	14.2	17.0	5.2	2.6	4.2	11.0	9.0	12.5	19.9	16.6	12.7	14.0	12.9	11.3
5 *m.*	4.1	10.5	13.7	15.0	5.1	2.6	4.2	7.5	8.2	7.0	16.5	16.5	12.6	12.0	12.9	11.3
10 *m.*	4.1	10.3	13.2	13.8	5.0	2.6	4.2	4.9	5.4	6.4	13.4	16.1	12.5	10.2	12.1	11.2
15 *m.*	4.1	9.8	12.0	13.0	4.8	2.6	4.2	4.4	5.0	5.8	10.8	15.0	12.4	7.5	12.0	11.2
25 *m.*	4.1	9.0	10.0	7.0	4.6	2.7	4.2	4.2	4.7	5.1	6.6	12.1	12.4	6.6	11.4	7.2
50 *m.*	4.1	6.1	5.2	5.0	4.7	2.8	3.8	4.2	4.0	4.7	5.2	4.9	11.9	5.4	8.9	5.6
100 *m.*	4.0	4.7	5.0	4.9	4.8	2.9	3.3	4.1	4.0	3.9	4.7	4.6	6.2	4.5	5.0	4.9
140 *m.*	4.0	4.5	4.9	4.9	4.8	3.0	3.3	4.1	4.0	4.1	4.1	4.1	4.3	4.8	4.8	4.8
	Secchi disc, *metres*															
	4.6	4.0	4.1	4.0	5.0	3.0	3.9	3.9	—	3.3	0.3	0.3	2.3	1.8	1.1	1.5

TABLE C.—Numbers of plankters in total vertical hauls at Station 31, Great Slave Lake, 1946 (Phytoplankters in thousands of cells).

	June 17	July 1	July 7	July 14	July 21	July 28	Aug. 3	Aug. 19	Aug. 27	Sept. 2	Av.	%
Nauplii	4,000	4,680	1,880	8,000	6,760	10,160	1,680	3,640	640	5,200	4,760	57.0
Diaptomus	1,200	1,040	1,040	4,880	1,080	2,920	1,600	4,320	400	4,560	2,304	27.6
Cyclops	720	760	920	2,760	680	1,720	320	560	160	372	897	10.8
Limnocalanus	560	360	200	720	412	348	172	274	80	132	326	3.9
Senecella	0	1	0	0	0	1	0	3	1	0	+	+
Epischura	0	0	0	108	0	0	13	0	0	0	12	0.1
Daphnia	0	0	0	13	80	13	27	76	27	160	40	0.5
Total Entomostraca	6,480	6,840	4,040	16,481	9,012	15,161	3,812	8,870	1,267	10,424	8,339	
Keratella	100	100	92	372	424	1,200	640	834	240	1,200	510	26.8
Kellicottia	60	60	68	228	160	960	600	760	80	1,000	398	20.9
Polyarthra	0	0	0	132	52	348	92	56	27	40	75	3.9
Asplanchna	60	0	0	0	40	412	80	212	27	332	116	6.1
Synchaeta	6,360	360	13	0	0	0	720	520	68	0	804	42.3
Total rotifers	6,580	520	173	732	676	2,920	2,132	2,382	442	2,572	1,903	
Total zooplankters	13,060	7,360	4,213	17,213	9,688	18,081	5,944	11,252	1,709	12,996	10,242	
Melosira	15,125	13,100	23,200	1,365	390	4,200	312	270	837	1,800	6,060	74.5
Asterionella	89	58	704	64	120	780	109	630	380	3,360	629	7.7
Fragilaria	0	0	0	450	60	88	150	168	175	270	136	1.7
Stephanodiscus	3	2	2	3	0	0	0	3	0	6	2	0.0
Synedra	3	4	8	10	14	8	8	114	128	126	42	0.5
Tabellaria	0	0	200	0	5	150	13	680	425	2,100	357	4.4
Anabaena	0	0	0	0	0	50	0	54	125	60	29	0.2
Dinobryon	0	0	0	62	1,300	4,610	850	790	950	180	874	10.7
Ceratium	0	0	0	0	0	3	0	6	10	3	2	0.0
Codonella	0	10	0	0	0	0	0	0	0	9	2	0.0
Total phytoplankters	15,220	13,174	24,114	1,954	1,888	9,889	1,442	2,715	3,030	7,914	8,133	

TABLE D.—Numbers of plankters in total vertical hauls at Station 31, Great Slave Lake 1947 (Phytoplankters in thousands of cells).

	June 25	July 3	July 9	July 17	July 23	Aug. 5	Aug. 12	Aug. 22	Aug. 27	Sept. 2	Sept. 9	Sept. 21	Av.	%
Nauplii	4,280	3,880	2,320	5,800	2,560	1,440	456	880	840	1,240	1,160	1,240	2,175	44.9
Diaptomus	960	840	960	1,760	520	492	172	2,360	1,560	2,440	2,400	4,800	1,605	33.2
Cyclops	1,000	800	920	840	332	1,080	240	584	532	492	388	1,160	697	14.4
Limnocalanus	13	360	200	960	292	120	66	560	264	572	148	26	298	6.2
Senecella	0	0	0	0	0	0	2	2	12	2	5	8	3	.1
Daphnia	13	0	0	0	13	0	13	0	0	53	0	66	13	.3
Bosmina	13	26	0	26	13	26	40	13	26	0	13	264	38	.8
Total Entomostraca	6,279	5,906	4,400	9,386	3,730	3,158	987	4,397	3,222	4,797	4,109	7,556	4,827	
Keratella	264	424	240	320	440	1,560	2,040	840	920	1,680	1,224	12,040	1,833	52.9
Kellicottia	216	480	120	480	280	600	424	492	652	2,240	1,348	3,520	904	26.1
Polyarthra	0	0	0	0	68	572	624	53	0	452	53	360	182	5.2
Asplanchna	0	0	0	0	0	66	66	0	53	148	13	624	81	2.3
Synchaeta	40	1,360	120	172	266	544	464	132	40	400	332	1,760	469	13.5
Total rotifers	520	2,264	480	972	1,054	3,342	3,618	1,517	1,665	4,920	2,970	18,304	3,469	
Total zooplankters	6,799	8,170	4,880	10,358	4,784	6,500	4,607	5,916	4,899	9,719	7,084	25,868	8,296	
Melosira	5,260	8,120	3,220	34,100	5,160	2,740	3,110	2,000	1,890	1,710	1,131	4,500	6,082	70.3
Asterionella	472	1,340	608	2,952	1,300	1,696	1,288	1,080	864	2,736	800	11,404	2,211	25.5
Fragilaria	0	0	0	75	0	200	20	0	300	0	50	1,080	144	1.7
Stephanodiscus	8	2.5	0	3	5	12	6	5	0	12	0	17.5	6	.1
Synedra	22	7.5	2	0	7.5	32	2	32.5	15	10	7	21	13	.1
Tabellaria	20	0	10	0	0	0	0	0	0	110	0	0	12	.1
Anabaena	20	0	0	0	0	0	20	125	90	440	550	735	165	1.9
Dinobryon	30	50	0	0	0	20	20	0	90	60	0	0	23	.3
Ceratium	2	0	0	0	0	0	0	2.5	0	0	0	0	0.3	+
Codonella	0	0	0	0	0	14	2	0	6	2	0	3.5	2.	+
Total phytoplankters	5,834	9,520	3,840	37,130	6,472.5	4,714	4,468	3,245	3,255	5,080	2,538	17,811	8,659	

Table E.—Numbers of plankters in total vertical hauls at Station 31 Great Slave Lake, 1948 (Phytoplankters in thousands of cells).

	June 26	July 1	July 14	July 22	July 31	Aug. 6	Aug. 11	Aug. 27	Sept. 11	Av.	%
Nauplii	11,600	7,520	4,420	4,200	1,200	2,220	1,800	810	1,610	3,931	51.5
Diaptomus	2,320	1,240	520	1,320	1,560	3,430	2,130	2,910	4,920	2,261	29.6
Cyclops	2,280	1,120	870	900	780	930	640	216	785	947	12.4
Limnocalanus	732	1,144	540	378	276	310	280	120	165	438	5.7
Senecella	1	1	0	0	0	0	0	0	0		
Daphnia	12	0	0	0	0	120	0	0	30	18	0.2
Bosmina	12	0	0	0	216	0	0	18	96	38	0.5
Total Entomostraca	16,957	11,025	6,350	6,798	4,032	7,010	4,850	4,074	7,606	7,633	
Keratella	264	148	240	440	690	636	584	420	954	486	34.0
Kellicottia	264	40	260	380	780	1,080	990	78	1,480	596	41.7
Polyarthra	0	0	0	0	156	696	370	0	96	146	10.2
Asplanchna	0	0	0	0	76	36	24	0	66	22	1.5
Synchaeta	80	64	0	0	396	436	310	198	124	179	12.5
Total rotifers	608	252	500	820	2,098	2,884	2,278	696	2,720	1,429	
Total zooplankters	17,565	11,277	6,850	7,618	6,130	9,894	7,128	4,770	10,326	9,062	
Melosira	6,730	5,018	5,038	1,790	1,820	1,410	1,660	1,140	5,700	3,367	82.5
Asterionella	495	435	475	360	645	156	168	210	1,080	447	10.9
Fragilaria	38	186	0	415	260	0	120	300	450	197	4.8
Stephanodiscus	0	0	0	0	0	0	4	8	8	2	
Synedra	8	8	4	8	4	3	0	0	15	6	0.1
Tabellaria	0	18	0	0	75	0	0	0	150	27	0.7
Anabaena	0	75	40	0	75	0	0	0	0	21	0.5
Dinobryon	0	0	0	40	70	0	30	0	0	15	0.4
Ceratium	0	0	4	0	4	9	2	0	0	2	
Codonella	0	0	8	0	0	0	0	0	0	1	
Total phytoplankters	7,271	5,740	5,569	2,613	2,953	1,578	1,984	1,658	7,403	4,085	

TABLE F.—Numbers of plankters in total vertical hauls at Station 31 Great Slave Lake, 1951 (Phytoplankters in thousands of cells).

	July 17	Aug. 5	Aug. 10	Aug. 31	Av.	%
Nauplii	978	3,858	2,016	180	1,758	36.3
Diaptomus	156	3,558	5,100	180	2,248	46.4
Cyclops	60	1,116	1,098	36	577	11.1
Limnocalanus	78	336	480	60	238	04.9
Daphnia	0	0	18	18	9	00.2
Bosmina	0	36	0	0	9	00.2
Total Entomostraca	1,272	8,904	8,712	474	4,840	
Keratella	120	876	618	336	487	38.5
Polyarthra	0	36	36	300	93	07.4
Kellicottia	78	798	918	240	508	40.2
Asplanchna	0	216	198	78	123	10.0
Synchaeta	78	60	0	60	49	03.9
Total rotifers	276	1,986	1,770	1,014	1,260	
Total zooplankters	1,548	10,890	10,482	1,488	6,100	
Melosira	21,025	2,660	3,430	3,260	7,594	78.8
Asterionella	2,560	1,340	1,810	1,560	1,067	11.1
Fragilaria	600	160	0	100	215	02.1
Stephanodiscus	0	0	4	0	1	+
Synedra	10	0	2	10	5	+
Tabellaria	0	0	0	0	0	00.0
Anabaena	0	0	0	910	228	02.4
Dinobryon	0	590	420	1,140	538	05.5
Ceratium	0	0	0	0	0	00.0
Codonella	0	2	4	0	2	+
Total phytoplankters	24,195	4,752	5,670	6,980	9,650	

TABLE G.—Numbers of plankters in total vertical hauls at Station 31 Great Slave Lake, 1952 (Phytoplankters in thousands of cells).

	July 13	July 22	Aug. 4	Aug. 11	Aug. 22	Sept. 2	Av.	%
Nauplii	9,704	11,812	704	264	1,120	2,800	4,400	61.9
Diaptomus	2,784	4,132	704	212	1,480	984	1,716	24.1
Cyclops	492	640	144	12	332	1,532	525	7.4
Limnocalanus	812	1,024	212	92	412	92	441	6.2
Daphnia	12	12	24	0	12	52	19	.3
Bosmina	0	12	52	0	0	0	11	.1
Total Entomostraca	13,804	17,632	1,840	580	3,356	5,460	7,112	
Keratella	304	1,080	292	132	1,320	4,664	1,299	24.3
Polyarthra	0	40	0	12	1,412	104	261	4.9
Kellicottia	212	960	264	104	2,424	1,532	916	17.2
Asplanchna	12	184	200	252	3,424	7,652	1,954	36.6
Synchaeta	1,092	1,852	504	412	0	1,600	910	17.0
Total rotifers	1,620	4,116	1,260	912	8,580	15,552	5,340	
Total zooplankters	15,424	21,748	3,100	1,492	11,936	21,012	12,452	
Melosira	2,137	10,537	1,625	3,012	2,875	2,487	3,779	54.7
Asterionella	1,020	3,100	2,000	1,565	2,780	320	1,797	26.0
Fragilaria	0	0	0	0	100	0	17	0.2
Stephanodiscus	0	0	0	0	0	5	1	+
Synedra	0	0	10	0	12	12	6	0.1
Tabellaria	12	75	50	137	837	343	243	3.5
Anabaena	0	0	0	25	462	25	85	1.2
Dinobryon	1,862	2,250	975	350	400	50	981	14.2
Ceratium	0	2	0	0	0	2	1	+
Codonella	0	5	0	0	0	0	1	+
Total phytoplankters	5,031	15,969	4,660	5,089	7,466	3,244	6,911	

TABLE H.—Numbers of plankters in total vertical hauls at Station 31 Great Slave Lake, 1953 (Phytoplankters in thousands of cells).

	July 13	July 25	Aug. 8	Aug. 19	Sept. 1	Av.	%
Nauplii	5,320	4,860	1,460	1,200	220	2,613	44.6
Diaptomus	880	6,700	1,940	2,000	120	2,328	39.9
Cyclops	340	1,480	280	540	80	544	9.3
Limnocalanus	440	760	240	240	60	348	6.0
Daphnia	0	0	0	20	40	12	0.2
Bosmina	0	0	0	0	0		
Total Entomostraca	6,980	13,800	3,920	4,000	520	5,844	
Keratella	400	1,100	3,020	2,920	340	1,556	29.4
Polyarthra	20	20	180	680	0	180	3.4
Kellicottia	40	2,120	1,380	1,140	20	940	17.8
Asplanchna	240	1,740	3,820	2,340	100	1,648	31.1
Synchaeta	0	0	360	4,340	140	968	18.4
Total rotifers	700	4,980	8,760	11,420	600	5,292	
Total zooplankters	7,680	18,780	12,680	15,420	1,120	11,136	
Melosira	3,307	8,900	1,960	2,460	412	3,328	65.4
Asterionella	1,400	2,380	392	408	60	1,028	20.2
Fragilaria	2,485	600	80	80	0	649	12.7
Stephanodiscus	0	2	0	0	0	+	+
Synedra	3	7	6	2	0	4	0.1
Tabellaria	148	50	0	0	0	40	0.8
Anabaena	35	0	0	0	0	7	0.1
Dinobryon	0	175	0	0	0	35	0.7
Ceratium	0	0	0	0	0		
Codonella	0	2	0	2	0		
Total phytoplankters	7,379	12,616	2,438	2,952	472	5,092	

TABLE I.—Numbers of plankters in total vertical hauls at Station 31, Great Slave Lake, 1954 (Phytoplankters in thousands of cells).

	July 3	July 11	July 17	July 26	Aug. 2	Aug. 9	Aug. 16	Aug. 24	Sept. 3	Sept. 11	Sept. 15	Av.	%
Nauplii	180	10,710	9,200	1,120	1,640	2,040	2,360	4,480	720	480	1,840	3,161	35.3
Diaptomus	495	3,960	1,640	640	640	5,200	3,400	23,600	1,120	1,230	2,720	4,059	45.4
Cyclops	315	1,800	40	160	40	300	880	5,160	200	270	1,760	993	11.1
Limnocalanus	585	900	360	1,340	360	900	440	560	68	90	235	540	6.0
Senecella	0	0	0	0	0	6	2	3	0	0	0	1	+
Daphnia	0	0	0	24	0	0	80	960	4	0	400	134	1.5
Bosmina	0	90	0	20	120	0	40	240	2	0	160	61	0.7
Total Entomostraca	1,575	17,460	11,240	3,404	2,800	8,446	7,202	35,003	2,114	2,070	7,115	8,949	
Keratella	0	630	320	960	1,160	50	640	16,160	320	840	7,280	2,578	58.0
Kellicottia	0	0	80	320	400	350	1,840	2,880	160	1,530	2,800	942	21.2
Synchaeta	0	360	80	480	1,120	0	240	0	120	270	1,120	344	7.7
Polyarthra	0	0	40	160	520	200	920	1,440	200	720	1,760	542	12.3
Asplanchna	0	0	0	32	0	50	80	0	0	30	80	25	0.6
Conochilus	0	0	0	0	0	0	0	0	80	30	0	10	0.2
Total rotifers	0	990	520	1,952	3,200	650	3,720	20,480	880	3,420	13,040	4,441	
Total zooplankters	1,575	18,450	11,760	5,356	6,000	9,096	10,922	55,483	2,994	5,490	20,155	13,390	
Melosira	129,500	119,500	17,420	2,170	9,630	2,410	1,290	5,700	1,460	352	1,180	26,418	89.0
Asterionella	320	160	88	50	3,210	1,860	2,375	9,600	2,224	815	3,552	2,205	7.4
Fragilaria	0	0	50	28	0	40	90	108	540	360	440	151	0.5
Stephanodiscus	0	0	2	0	24	0	3	0	0	0	0	3	+
Synedra	10	0	7	12	48	12	18	18	4	16	20	15	+
Tabellaria	0	0	0	4	0	0	15	2,320	40	500	2,500	489	1.6
Anabaena	0	0	0	0	0	0	0	0	0	280	0	25	0.1
Dinobryon	0	0	0	120	120	0	0	3,560	0	40	440	389	1.3
Ceratium	0	0	2	2	0	9	27	9	8	158	40	23	0.1
Codonella	0	0	2	0	24	18	3	0	2	0	8	5	+
Total phytoplankters	129,830	119,660	17,571	2,386	13,056	4,349	3,821	21,315	4,278	2,521	8,180	29,723	

TABLE J.—Plankters in total vertical hauls at stations in the open portion of Great Slave Lake, 1944 to 1947 (Phytoplankters in thousands of cells).

	Station 3 June 26/44 44 m.	Station 27 Aug. 2/45 68 m.	Station 32 June 18/46 23 m.	Station 33 June 22/46 90 m.	Station 38 June 18/46 105 m.	Station 55 Aug. 7/47 65 m.	Station 56 Aug. 7/47 115 m.	Station 57 Aug. 7/47 99 m.	Average	%
Nauplii	172	180	700	4,860	7,200	2,980	6,140	320	2,819	43.3
Diaptomus	384	1,140	200	780	2,000	8,020	6,460	1,040	2,503	38.5
Cyclops	52	840	240	420	760	1,420	1,260	520	689	10.6
Limnocalanus	732	100	40	320	920	960	240	212	440	6.8
Daphnia	—	—	—	—	—	—	60	184	30	0.5
Bosmina	—	20	20	—	—	20	20	64	18	0.3
Total Entomostraca	1,340	2,280	1,200	6,380	10,880	13,400	14,180	2,340	6,499	
Keratella	13	100	40	160	20	540	1,080	384	292	19.8
Kellicottia	26	520	—	180	—	1,200	2,180	1,452	695	47.1
Polyarthra	—	20	20	20	60	120	160	40	55	3.7
Asplanchna	—	—	—	—	60	20	180	1,160	178	12.1
Synchaeta	—	20	260	620	100	140	420	480	255	17.3
Total rotifers	39	660	320	980	240	2,020	4,020	3,516	1,475	
Total zooplankters	1,379	2,940	1,520	7,360	11,120	15,420	18,200	5,856	7,974	
Melosira	8,175	1,650	24,952	11,480	15,560	7,200	3,250	9,630	10,236	95.8
Asterionella		456	294	176	64	456	1,056	312	352	3.3
Fragilaria	—	—	—	20	180	60	40	—	38	0.3
Stephanodiscus	2	6	—	—	—	6	—	6	2	+
Synedra	—	3	—	—	—	—	2	6	1	+
Tabellaria	—	15	—	—	—	—	—	15	4	+
Anabaena	—	180	—	—	—	—	—	—	22	0.2
Dinobryon	—	—	—	—	—	—	260	—	32	0.3
Codonella	—	3	—	—	—	6	2	—	1	+
Total phytoplankters	8,177	2,313	25,246	11,676	15,804	7,728	4,610	9,969	10,688	

TABLE K.—Plankters in total vertical hauls at stations near Resolution and along the southwest shore of Great Slave Lake, 1944 to 1947 (Phytoplankters in thousands of cells).

	Sta. 1 June 23/44 11 m.	Sta. 2 June 25/44 30 m.	Sta. 26 July 30/45 15 m.	Sta. 1 June 16/46 11 m.	Sta. 2 June 17/46 30 m.	Sta. 2 July 4/47 30 m.	Average	%
Nauplii	340	1,100	680	130	960	1,260	745	54.6
Diaptomus	34	240	140	240	440	200	216	15.8
Cyclops	11	160	500	20	260	200	192	14.0
Limnocalanus	8	1,040	—	—	120	80	208	15.2
Epischura	—	10	—	—	10	—	3	0.2
Daphnia	—	—	—	—	—	20	3	0.2
Total Entomostraca	393	2,550	1,320	390	1,790	1,760	1,367	
Keratella	20	—	380	60	40	240	123	27.0
Kellicottia	40	—	—	—	20	80	23	5.1
Polyarthra	—	—	640	10	—	20	112	24.6
Asplanchna	—	—	520	—	—	—	87	19.1
Synchaeta	—	—	160	60	280	160	110	24.2
Total rotifers	60	—	1,700	130	340	500	455	
Total zooplankters	453	2,550	3,020	520	2,130	2,260	1,822	
Melosira	1,515	6,270	3,712	3,970	17,850	8,050	6,894	95.8
Asterionella	432	2	440	16	272	464	271	3.8
Fragilaria	—	—	—	—	2	—	+	+
Stephanodiscus	2	—	8	—	—	—	2	+
Synedra	—	—	2	—	—	—	+	+
Tabellaria	15	—	38	—	—	—	9	+
Dinobryon	—	—	—	—	—	120	20	0.3
Codonella	—	2	—	—	4	—	1	0.1
Total phytoplankters	1,964	6,274	4,200	3,986	18,128	8,634	7,197	

TABLE L.—Plankters in total vertical hauls at stations near the Outpost Islands and one in the north arm, Great Slave Lake, 1944 to 1946 (Phytoplankters in thousands of cells).

	Sta. 18 July 27/45 97 m.	Sta. 20 July 10/45 3 m.	Sta. 21 July 11/45 23 m.	Sta. 22 July 10/45 36 m.	Sta. 40 Aug. 6/46 40 m.	Sta. 8 July 27/44 35 m.
Nauplii	560	260	2,300	2,320	4,640	2,340
Diaptomus	460	40	120	480	1,520	6,340
Cyclops	140	—	180	160	3,860	980
Limnocalanus	240	—	120	120	260	180
Daphnia	—	20	—	—	520	—
Bosmina	—	—	—	—	220	120
Total Entomostraca	1,400	320	2,720	3,080	11,020	9,960
Keratella	40	80	40	40	7,860	1,800
Kellicottia	60	20	60	120	2,920	3,880
Polyarthra	20	—	—	—	6,120	180
Asplanchna	—	—	—	—	40	3,040
Synchaeta	20	20	20	80	3,820	1,400
Total rotifers	140	120	120	240	20,760	10,300
Total zooplankters	1,540	440	2,840	3,320	31,780	20,260
Melosira	950	1,140	2,930	2,162	4,415	1,900
Asterionella	128	136	112	320	720	480
Fragilaria	—	620	—	100	210	—
Stephanodiscus	—	—	—	—	3	—
Synedra	6	4	2	2	117	12
Tabellaria	—	—	—	50	645	—
Anabaena	—	—	—	—	210	25
Dinobryon	—	—	—	—	30	—
Ceratium	—	—	—	—	51	—
Codonella	—	2	—	—	—	—
Total phytoplankters	1,084	1,902	3,044	2,634	6,401	2,417

TABLE M.—Plankters in total vertical hauls at stations in Yellowknife Bay, Great Slave Lake, 1944 to 1946 (Phytoplankters in thousands of cells).

	Station 5 Aug. 25/44 63 m.	Station 7 July 11/44 12 m.	Station 5 July 16/45 63 m.	Station 7 July 14/45 12 m.	Station 16 July 18/45 13 m.	Station 23 July 20/45 1 m.	Station 24 July 21/45 3 m.	Station 5 July 29/46 63 m.	Station 5 Aug. 10/46 63 m.	Average	%
Nauplii	1,560	80	420	620	132	100	100	400	2,540	661	31.1
Diaptomus	2,720	180	60	40	52	20	—	780	4,080	881	41.5
Cyclops	720	—	120	400	252	40	20	140	920	290	13.6
Limnocalanus	360	—	100	—	92	—	—	220	420	132	6.2
Daphnia	160	—	—	—	12	—	—	—	20	21	1.0
Bosmina	480	140	40	220	40	120	40	60	100	138	6.5
Total Entomostraca	6,000	400	740	1,280	580	280	160	1,600	8,080	2,123	
Keratella	1,080	460	340	660	344	380	700	880	2,040	765	19.1
Kellicottia	560	100	660	520	424	40	20	240	1,120	409	10.0
Polyarthra	920	1,812	700	2,920	1,440	1,620	2,280	1,960	1,060	1,635	40.4
Asplanchna	40	160	200	340	120	—	40	—	80	109	2.7
Synchaeta	220	440	440	1,700	200	3,080	1,340	1,220	1,540	1,131	27.9
Total rotifers	2,820	2,972	2,340	6,140	2,528	5,120	4,380	4,300	5,840	4,049	
Total zooplankters	8,820	3,372	3,080	7,420	3,108	5,400	4,540	5,900	13,920	6,172	
Melosira	2,560	510	1,210	1,080	1,270	400	165	43,500	14,250	7,216	80.4
Asterionella	4,192	240	416	208	216	224	240	352	608	744	8.3
Fragilaria	40	—	—	—	—	—	—	—	—	4	+
Stephanodiscus	20	—	—	—	—	—	—	4	—	3	+
Synedra	—	—	8	4	—	22	8	—	—	5	+
Tabellaria	800	40	—	—	40	40	82	80	220	145	1.6
Anabaena	200	—	—	—	—	—	30	—	120	39	.4
Dinobryon	160	150	—	—	—	100	30	960	6,000	822	9.1
Ceratium	4	—	—	—	—	—	—	—	8	1	+
Codonella	12	—	—	—	—	—	—	—	—	1	+
Total phytoplankters	7,988	940	1,634	1,292	1,526	786	555	44,896	21,206	8,980	

TABLE N.—Plankters in total vertical hauls at Station 35, Christie Bay, 1946 and 1947.

	1946				1947					
	July 3	July 18	Aug. 1	Aug. 30	July 11	July 17	Aug. 13	Aug. 21	Av.	%
Nauplii	920	635	240	252	2,900	1,973	567	30	939	60.0
Diaptomus	225	160	320	78	470	631	80	310	284	18.3
Cyclops	137	55	70	6	670	443	107	40	191	12.3
Limnocalanus	31	27	140	9	46	61	436	130	110	7.1
Senecella	9	4	11	—	7	13	2	2	6	0.4
Epischura	—	—	—	—	—	19	1	—	2	0.1
Daphnia	3	—	—	36	30	16	23	30	17	1.0
Bosmina	—	—	—	1	—	—	—	—	+	+
Total Entomostraca	1,325	881	781	382	4,123	3,157	1,217	542	1,549	
Kellicottia	—	5	160	83	—	18	107	70	55	34.8
Keratella	—	—	40	26	—	3	39	40	18	11.4
Conochilus	—	5	60	19	—	13	—	410	64	40.5
Synchaeta	—	—	20	52	—	5	—	—	9	5.7
Asplanchna	—	—	10	69	—	—	—	—	10	6.3
Polyarthra	—	—	—	9	—	—	10	—	2	1.3
Total rotifers	—	10	290	258	—	39	156	520	158	
Asterionella	1,736	11,640	36,280	91,280	8,400	8,760	9,768	5,680	21,693	51.3
Eunotia	217	1,440	2,310	1,120	6,100	588	80	240	1,512	3.6
Melosira	375	600	700	4,200	5,750	370	—	1,600	1,699	4.0
Tabellaria	1,120	1,600	2,100	30,100	—	100	650	1,350	4,628	11.0
Fragilaria	—	1,200	—	2,100	—	1,550	—	400	656	1.6
Stephanodiscus	—	80	—	70	—	4	53	60	33	0.1
Synedra	—	—	350	630	—	—	—	110	136	0.3
Anabaena	—	—	—	5,600	—	—	—	—	700	1.7
Dinobryon	210	1,600	50,400	34,300	1,500	30	130	—	11,021	26.1
Ceratium	—	—	—	840	50	6	153	180	154	0.3
Codonella	—	—	—	—	—	5	16	—	3	+
Total phytoplankton	3,658	18,160	92,140	170,240	21,800	11,413	10,850	9,620	42,235	

TABLE O.—Plankters in total vertical hauls at Station 36, Christie Bay, 1946 and 1947.

	1946		1947	
	July 19	Aug. 19	July 18	Aug. 14
Nauplii	5,329	2,861	2,707	2,366
Diaptomus	717	262	386	769
Cyclops	315	105	211	208
Limnocalanus	254	228	54	138
Senecella	36	13	17	16
Epischura	2	13	4	4
Daphnia	13	30	1	112
Bosmina	4	2	2	1
Total Entomostraca	6,670	3,415	3,382	3,614
Kellicottia	4	67	3	3
Keratella	2	18	10	7
Conochilus	1	23	1	69
Synchaeta	0	6	2	3
Total rotifers	7	114	16	142
Asterionella	25,328	124,000	1,555	2,780
Eunotia	1,260	980	2,594	730
Melosira	350	830	1,535	138
Tabellaria	1,120	7,200	103	76
Fragilaria	670	180	65	4
Stephanodiscus	0	20	14	0
Synedra	0	210	42	72
Dinobryon	4,320	34,400	0	22
Ceratium	0	190	7	4
Codonella	0	0	7	0
Total phytoplankters	33,048	168,010	5,922	3,826

TABLE P.—Plankters in total vertical hauls at stations in McLeod Bay, elsewhere in the east arm of Great Slave Lake and in Artillery Lake, 1944 to 1947. Phytoplankters recorded as total cells.

	Sta. 28 McLeod Bay Aug. 8/45	Sta. 29 McLeod Bay Aug. 13/45	Sta. 45 McLeod Bay July 19/47	Average McLeod Bay 3 stations	Sta. 14 Christie Bay July 21/44	Sta. 42 Wildbread Bay Aug. 21/46	Sta. A Artillery Lake Aug. 11/45
Nauplii	420	80	920	473	320	12,000	80
Diaptomus	510	400	1,120	677	260	3,600	80
Cyclops	15	260	60	112	780	80	300
Limnocalanus	88	80	190	119	20	108	—
Senecella	16	2	3	7	6	9	—
Daphnia	2	20	—	7	40	600	40
Bosmina	1	—	—	+	40	—	—
Total Entomostraca	1,052	842	2,293	1,395	1,446	16,397	500
Keratella	7	20	5	11	520	—	20
Kellicottia	24	100	30	51	1,160	200	180
Polyarthra	88	20	10	39	900	1,950	80
Asplanchna	—	—	—	—	20	1,200	—
Synchaeta	—	—	—	—	60	—	20
Total rotifers	119	140	45	101	2,660	3,350	300
Total zooplankters	1,171	982	3,338	1,496	4,106	19,747	800
Melosira	17,600	280,000	17,100	104,900	165,000	175,000	520,000
Asterionella	9,500	64,000	880	24,793	240,000	720,000	72,000
Fragilaria	660	15,000	1,100	5,587	—	25,000	—
Stephanodiscus	440	—	110	183	—	20,000	—
Synedra	44	1,500	—	514	7,500	—	6,000
Tabellaria	440	30,000	—	10,147	82,500	87,000	—
Eunotia	264	2,000	2,860	1,708	—	30,000	—
Anabaena	—	—	3,850	1,283	30,000	125,000	—
Dinobryon	—	110,000	—	36,666	30,000	3,830,000	1,000
Ceratium	—	—	—	—	—	172,000	—
Codonella	176	—	165	114	113	—	—
Total phytoplankters	29,124	502,500	26,065	185,885	555,113	5,184,000	599,000

Storage of Frozen Plaice Fillets[1,2]

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ABSTRACT

Taste panel assessments of taste, texture, and grade, and estimations of soluble actomyosin and of fat spoilage on plaice fillets after frozen storage at +10°F. (−12°C.) are reported. The plaice became unpalatable at 6 to 7 months as compared with 2 to 3 months for cod and about 8 months for Atlantic halibut at +10°F. Ascorbic acid was not effective in preventing lipid deterioration. A relationship between protein denaturation and the lipid content of the fish and its deterioration is suggested.

INTRODUCTION

Frozen fillets of American plaice, *Hippoglossoides platessoides*, have now been investigated in our continuing study of the changes occurring in frozen fish during cold storage. Previous studies (Dyer 1951, 1953) on Atlantic haddock, *Melanogrammus aeglefinus*; cod, *Gadus callarias*; and halibut, *Hippoglossus hippoglossus*, have shown that there are two major changes: first, the development of toughness, shown by taste panel assessment, and related to the amount of protein denaturation; and second, the development of off-flavours suggestive of fat spoilage.

As well as information on the storage life of frozen plaice, data are needed on the use of protein solubility as an index of quality in frozen fish, and on the relationships between protein solubility and lipid deterioration.

At present the only means available for reducing the degree of protein denaturation are storage at low temperature and the freezing of fresh material. This assumes proper packaging and prevention of desiccation. Antioxidants may prove of value in retarding the second change, the deterioration of the fatty fractions. Accordingly, the influence of ascorbic acid treatment was investigated.

Bauernfeind *et al.* (1948) report two experiments with frozen plaice and flounder fillets. They conclude that treatment with ascorbic acid resulted in a slight delay in the development of off-flavours in frozen flounder stored at 0°F. (−18°C.). However, most of the work on the retardation of rancidity in frozen fish by antioxidants, particularly by ascorbic acid, has concerned their effect on peroxide values of the fat and on colour. Tarr (1947) has shown the effectiveness of ascorbic acid in retarding peroxide development and in delaying the fading of the flesh pigments in such fish as salmon. In herring, Banks (1952) has found that while ascorbic acid treatment may sometimes inhibit the rise in peroxide values, it does not prevent the development of off-flavours or odours. In addition,

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[2]Paper No. 7 of a series "Proteins in fish muscle". The preceding paper appeared in **12**(5): 646–648, of this Journal (1955).

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he found that the ascorbic acid itself imparted an undesirable acid or metallic flavour to the fish.

The evidence available seems to indicate that ascorbic acid may be effective in retarding fat spoilage in some varieties of fish and not in others. Work is particularly needed to correlate the effect of the antioxidant with actual taste and flavour measurements as well as with chemical measurements of fat spoilage.

EXPERIMENTAL

Commercial fillets from American plaice were used. After filleting, they were washed and divided into two lots. One lot was immediately wrapped in cellophane and packed in 5-lb. (2.3-kg.) waxed cartons. Fillets from the second lot were dipped for 1 to 2 minutes in an ascorbic acid–Irish moss gel solution containing 0.3% ascorbic acid[3] and 0.5% dried Irish moss gel. After draining, these fillets were wrapped and packed as the others. Both lots were immediately frozen in Birdseye freezers in the premises of a local fish company. After freezing, they were removed to the cold rooms at this Station for storage at +10°F. (−12°C.).

Samples were removed at approximately 3-week periods for organoleptic and chemical examination.

The samples for the taste panel tests were prepared as outlined in previous work (Dyer and Dyer 1949). They were placed in the oven while still frozen, and baked for 13 minutes at 500°F. (260°C.). The score sheets and the method of scoring were similar to those used in the above work, except that scoring for texture, taste, odour, and grade only was used. Scoring was on the basis of numerical values of 0 to 5. Two samples were served at a time to a panel of eight tasters, and this was repeated three times for each set of samples. The tasters had all had some experience in tasting plaice fillets.

Chemical analyses for soluble protein nitrogen, actomyosin nitrogen, free fatty acid, and peroxide number of the fat were carried out on uncooked portions of each sample. Actomyosin nitrogen and soluble protein nitrogen were extracted by the method of Dyer *et al.* (1950) and the protein nitrogen estimated by the biuret method (Snow 1950). In addition, moisture, total nitrogen, and non-protein nitrogen were determined on several samples.

For determination of fat spoilage, a modification of the method used by Banks (1952) was used. To a 100-g. raw sample, cut in small pieces, was added 100 g. powdered anhydrous sodium sulphate and 200 ml. anhydrous chloroform. This mixture was blended in a Waring Blendor for about 30 seconds and filtered through sintered glass. Extracted fat was determined by evaporating 25 ml. of this chloroform extract to constant weight under vacuum in a boiling water bath, then weighing the residue. Free fatty acid was determined by adding 50 ml. alcohol–benzene (1:1) to 25 ml. of the extract and titrating with sodium hydroxide using phenolphthalein as indicator. The values were calculated as oleic acid.

The determination of peroxide values was similar to the methods used by

[3]Kindly donated by Merck and Co., Ltd., Montreal, P.Q.

Banks (1937), and Tarr (1947). Aliquots of 10 and 20 ml. of the filtrate were added to 30 ml. glacial acetic acid and 2 drops of fresh saturated potassium iodide solution. After this mixture had stood in the dark for 10 minutes, 50 ml. water and 2 ml. starch indicator solution were added, and the solution was immediately titrated with N/100 sodium thiosulphate. The peroxide value was calculated as milliequivalents per 100 g. fat, after subtracting the blank value.

Crude fat was determined by the method given in the A.O.A.C. (1950).

RESULTS

The moisture content of the stored fillets averaged 83%, total nitrogen 2.3%, and non-protein nitrogen 0.35%. "Albumin" nitrogen content was 0.5%, or 25% of the total protein nitrogen. These amounts did not change throughout the storage period.

The texture and taste remained constant up to about 6 to 10 weeks' storage, then declined fairly rapidly up to about 28 weeks. Thereafter texture showed little change but grading for taste rapidly dropped up to 32 weeks, when it levelled off at about 45%. There was very little difference between the control and ascorbic acid-treated samples.

The curves for the average grade, shown in Fig. 1, are close to the taste scores, showing little change up to 2 months, then a decline to 6 months, followed

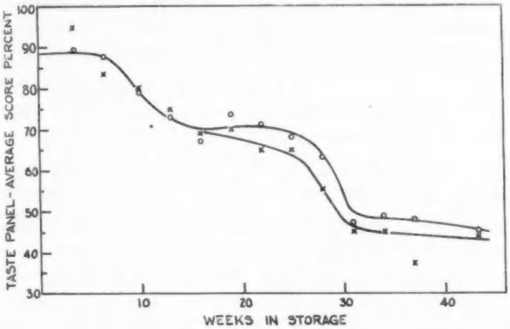

FIG. 1.—Average taste panel assessments on frozen plaice fillets stored at +10°F. (−12°C.).
O—control, ×—ascorbic acid-treated.

by a rapid drop at 7 months. At this time, 32 weeks, the samples had become definitely unacceptable, chiefly due to the development of off-flavours, together with some toughening and poor appearance. Visual examination showed little effect by ascorbic acid, although there was some yellowing of the treated samples after 36 weeks.

The changes in soluble actomyosin are shown in Fig. 2. The actomyosin curves were parallel to the soluble protein nitrogen curves, as had been usual with the other species investigated, actomyosin being the protein fraction which is easily denatured on frozen storage.

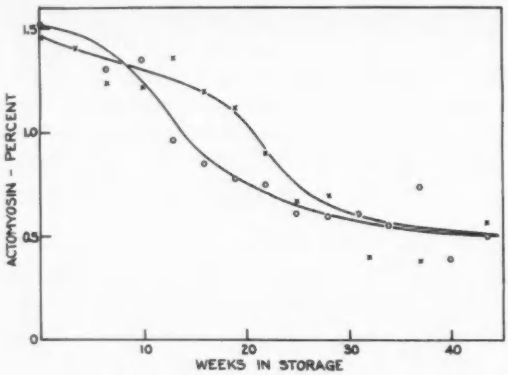

FIG. 2.—Soluble actomyosin as per cent nitrogen of fish in frozen plaice fillets stored at +10°F. (−12°C.).
O—control, ×—ascorbic acid-treated.

The actomyosin curves fell off gradually, reaching a plateau at about 30 weeks. It is seen that they decreased at a rather faster rate than the texture values which remained constant up to about 10 weeks and then dropped rapidly to a plateau at about 30 weeks. This agreed with previous results.

It is apparent that there is good agreement between the protein extractability and the texture values. Thus, protein solubility appears to be usable as a storage quality index, even in a fish showing considerably more lipid than cod.

The average crude fat content found varied from 1.1 to 1.9% with an average value of 1.5%. The free fatty acid, expressed as percentage oleic acid in the extracted fat, gradually increased up to about 25 weeks and then remained constant at a level of about 30 to 40% (Fig. 3). It is seen that there was a sharp drop in the palatability scores between 25 and 30 weeks, which appeared to be

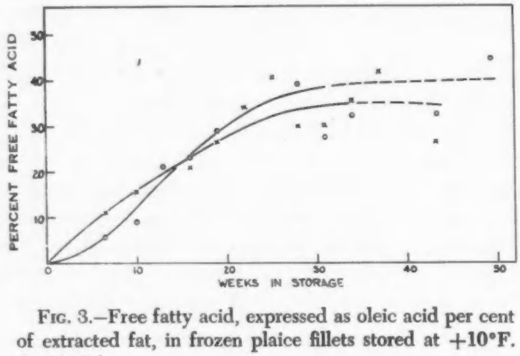

FIG. 3.—Free fatty acid, expressed as oleic acid per cent of extracted fat, in frozen plaice fillets stored at +10°F. (−12°C.).
O—control, ×—ascorbic acid-treated.

due to off-flavour development related to fat spoilage. There was no difference between the ascorbic acid and the control samples.

The values obtained for peroxides were not as clear cut. They remained essentially constant throughout at a level of 0 to 2 milliequivalents per 100 g. fat. Occasional single high values were obtained between 30 and 44 weeks but were not reproducible. Their significance is doubtful, but they may indicate possible changes in the lipid fraction at this stage.

There was no evidence that ascorbic acid treatment had any effect on the frozen plaice fillets, either on palatability as judged by the taste panel, or on lipid oxidation as measured by peroxide values or content of free fatty acids.

The results show that the frozen plaice used kept in an acceptable condition for about 6 months at +10°F. (−12°C.), in waxed cartons. The corresponding times were about 2 to 3 months for cod, and about 8 months for Atlantic halibut at this temperature. Presumably, the storage life of plaice at −10°F. (−23°C.) would be proportionately longer.

In the stored frozen plaice, as noted previously in other species, there was first a loss of solubility of the protein, followed by off-odour development.

It is interesting to note the rapid drop in the taste panel grade between 28 and 32 weeks, which was occasioned by the appearance of off-odours and flavours suggestive of fat spoilage. This occurred just at the point when the drop in protein solubility levelled off and when the fat or lipid hydrolysis had reached its maximum and also levelled off. It suggests a relation between the denaturation of the protein and the deterioration of the fat. This question will be discussed further in a later paper.

The soluble actomyosin levelled off at about 0.4 to 0.5%, expressed as nitrogen per 100 g. fish. Thus a considerable fraction (20 to 25% of the total protein nitrogen) of protein which is salt extractable and which will precipitate on dilution to 0.5% salt remained in this species even after 45 weeks. This compares with values approaching 0% in completely denatured cod, and about 20 to 40% (as percentage of total protein nitrogen) in halibut, although in the latter case the minimum may not have been reached at the time of termination of the experiment. There does, however, appear to be a contrast between cod on the one hand and the more fatty fishes, plaice and halibut, on the other. This point needs further investigation, but it appears to indicate that there must be something in the fatty fishes which inhibits denaturation or increases the dispersability or peptizability of the proteins in salt solutions, and, of course, lipid-type compounds are immediately suspected. It is known that this type of protein does form complexes with lipids and nucleic acids. (Claude, 1949; Szent-Gyorgyi, 1947; Hamoir, 1951). Lipoproteins and nucleoproteins are stated to be split by freezing repeatedly, but if the lipids were not destroyed by oxidation, a non-specific re-formation could take place on extraction. This might be more effective in the species with the higher lipid content where complete oxidation is unlikely in the presence of a limited oxygen supply. The formation of certain free fatty acids or other oxidation products might result in more effective protection of the protein.

Another consideration is what happens to actomyosin under frozen storage. It has been shown (Johnson and Landolt, 1951) that actomyosin is dissociated into its components by high salt concentration. Thus, freezing might be expected to dissociate the actomysin, and we may be dealing with the actin and myosin components in frozen storage. On extraction, these proteins, unless aggregated, would both be soluble in salt solution. It is possible that in the original actomyosin *in situ* the lipids may prevent dissociation, or non-specific lipid–protein complexes may be formed on extraction which are peptizable in salt and precipitable by dilution. It is, perhaps, more probable that the surface-active lipids, or some of their oxidation or hydrolysis products, would modify the peptizability of the proteins, resulting in the apparently less complete denaturation of the proteins in the case of the more fatty fish.

SUMMARY

Plaice fillets stored frozen at +10°F. (−12°C.) became unpalatable at 6 to 7 months, as shown by taste panel assessments, compared with 2 to 3 months for cod and about 8 months for Atlantic halibut. The texture ratings showed an increase in toughness parallel to the decrease in extractable actomyosin content, followed closely by the development of off-odours and flavours correlating with lipid deterioration. Treatment with ascorbic acid gave no improvement under the conditions used. Extractable actomyosin appeared to be a useful quality index. A relationship between protein denaturation and the lipid content and its deterioration is suggested and discussed.

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The Collapse and Recovery of a Small Whitefish Fishery[1]

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ABSTRACT

Pigeon Lake, Alberta, is a shallow eutrophic lake with a sandy basin, gentle contours and an area of 40 square miles. It contains whitefish, pike, yellow walleye, perch, burbot, white suckers and spottail shiners. The whitefish have been commercially exploited for many years and catch statistics are available from 1918.

In 1941 a greatly increased catch of whitefish was permitted. Large annual yields continued until 1946; in 1947, in spite of considerable effort, a very small catch was made. Since this collapse fishing was prohibited in two years and light in two years. The lake now contains a normal whitefish population.

Samples of the commercial catch during this period showed that the average age of the fish fell from 5.1 to 2.3 years, then, after collapse, increased to 5.7 years. Growth rates increased greatly, then decreased to the original level. Age at maturity decreased from five to two years.

Calculations of the number of fish each year-class contributed to the fishery reveal that the collapse of the fishery was not due to overfishing; the weak year-classes which caused the collapse had parent year-classes of normal abundance. It is suggested that egg destruction by strong winds may have caused the weak year-classes.

CONTENTS

INTRODUCTION

Pigeon Lake, Alberta, has an area of 40 square miles. It lies in a sandy basin with gentle contours and low shore development. Depths do not exceed 30 to 40 feet. It drains by a small creek into the Battle River.

The fish population of Pigeon Lake consists of whitefish (*Coregonus clupeaformis* (Mitchill)), yellow walleye (*Stizostedion vitreum* (Mitchill)), yellow

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perch (*Perca flavescens* (Mitchill)), northern pike (*Esox lucius* L.), white sucker (*Catostomus commersoni* (Lacépède)), burbot (*Lota lota* (Linnaeus)), and the spottail shiner (*Notropis hudsonius* (Clinton)).

The whitefish have been commercially fished for many years and statistics are available from 1918.

The smallness and the shape of the lake ensure that the whitefish are of one population, i.e., that separate inshore and offshore groups, or populations confined to certain bays or areas do not exist. The nature of the drainage precludes the possibility of recruitment from outside the lake. The absence of ciscoes or any other competitor species except white suckers, and a very low predation rate of pike and yellow walleyes on whitefish contribute to the relatively simple ecological picture. Pigeon Lake is thus a good lake in which to observe the effects of exploitation of whitefish; many of the variables which complicate the interpretations of fluctuations in population abundance are here reduced to as low a minimum as is possible in a natural environment.

Observations on the whitefish of Pigeon Lake were begun in 1942 and have continued to the present time. Four papers have been published in which some of these observations are included (Miller, 1946, 1947, 1949, 1952). In the present study these data are brought together and interpreted in the light of more recent observations. The Pigeon Lake fishery passed through a long initial period of light exploitation; this was followed by six years of heavy exploitation. At the end of this period the fishery collapsed. The collapse appeared to be caused by overfishing; the fish were much younger and growing at considerably faster rates than during the period of low fishing pressure. However, following the collapse, the fishery recovered and whitefish are again abundant. Data on age composition during the recovery period reveal that the collapse was probably not due to reduction of brood stock.

Recently a number of authors (notably Ricker, 1954) have pointed out that recruitment in animal populations may be strongly density-dependent; i.e., strong year-classes may result from low parental numbers whereas weaker filial generations may arise from large breeding populations. The main purpose of the present study is to offer further evidence of the truth of this generalization; and to emphasize that reduction of brood stock in a whitefish fishery is an unlikely cause of declining productivity.

MATERIAL AND METHODS

The study is based on the age composition of 13 samples of whitefish removed from Pigeon Lake each year from 1942 to 1954. Altogether 2,138 fish have been taken in the samples. All samples were taken during fall and early winter, either immediately preceding the commercial fishing season or during the season. The commercial fishery uses 5½-inch mesh gill nets and all the samples were taken with this size of net. The samples are thus believed to be representative of the exploited portion of the population.

RELIABILITY OF SAMPLES. The samples varied in size from 92 fish for the 1948–49 season to 330 fish for the 1943–44 season (Table III). The reliability of

the smaller samples may be established by examining some of the larger ones, which consist of several small samples added together. The 1943–44 sample of 330 fish was made up of four groups as follows: December 2, 66 fish; December 20, 88 fish; February 2–9, 98 fish; February 11–14, 78 fish. The age compositions of these samples and of the aggregate sample are shown in Table I. Age is the number of completed annuli.

TABLE I.—The age composition of four samples of whitefish taken in December, 1943 and February, 1944.

		Age				
	III	IV	V	VI	VII	r
Dec. 2	32	19	10	5	0	66
Dec. 20	26	35	20	5	2	88
Feb. 2–9	27	34	20	14	3	98
Feb. 11–14	27	26	13	9	3	78
c	112	114	63	33	8	330

The data in Table I are set up in the form of a contingency table. A chi-square test may be carried out to determine if the four samples are random samples with respect to age. The formula is, $\chi^2 = 330[\Sigma f^2/rc - 1]$, where f is the frequency in each cell.

Applying the formula to these data, a χ^2 value of 15.2 is obtained; with 12 degrees of freedom this gives a Probability of 0.23. Therefore, it is reasonable to conclude that the four samples are representative of the age distribution of the exploited portion of the population, within the limits of random sampling error.

The same test has been used on samples of 100 taken Dec. 4, 1946 and of 201 taken January 8, 1947; and on two samples of 92 and 125 fish taken Oct. 27, 1948 in different nets. Probabilities of 0.44 and 0.15 were obtained.

From the above it is concluded that samples of approximately 100 fish give an unbiased indication of the age composition of the commercially exploited portion of the population of Pigeon Lake.

TREATMENT OF SAMPLES. The fork length in inches, and the weight in ounces of each fish were recorded on an envelope. In the envelope were placed scales taken from the left side mid-way between dorsal fin and lateral line. In earlier years the scales were cleaned, mounted in glycerine jelly, and projected for study. In later years the dried scales were placed between two microslides and examined under a binocular microscope at magnifications of 50 and 100 diameters. Age was recorded as the number of completed annuli.

STATISTICS OF THE PIGEON LAKE FISHERY

The whitefish catch is limited by law; each year the total pounds of fish to be removed is decided before the fishing season begins in December. When fishing begins the local government inspector tallies each day's catches and, when the limit is reached, the lake is closed. In recent years a large number of

fishermen have usually removed the limit in a few days. When market prices are high and the fish seem to be abundant, an extension of the limit has often been permitted. From 1918 to 1939 the average catch was 179,000 pounds per year; 200,000 pounds was exceeded only five times during this period.

The war years saw an increased demand for fish; the good market offered an opportunity to experiment with Pigeon Lake. It was decided to permit more or less unlimited catches in order to discover just how much the lake would yield, and for how long. The catches since 1940 are shown in Table II.

TABLE II.—Whitefish catches in Pigeon Lake, in pounds.

Year[a]	Catch	No. of men fishing[b]	Year	Catch	No. of men fishing
1940–41	582,900	421	1947–48	Closed	0
1941–42	354,600	293	1948–49	63,800	296
1942–43	340,000	487	1949–50	Closed	0
1943–44	485,000	260	1950–51	66,000	379
1944–45	411,000	826	1951–52	187,400	731
1945–46	350,000	1,032	1952–53	231,000	1,041
1946–47	160,000	798	1953–54	200,000	615
			1954–55	336,400	445

[a]The fishing year is usually from December to February.
[b]Each man was allowed 100 yards of net until 1954–55, when 300 yards were permitted.

Table II shows that, freed from the government restriction, the catch rose immediately to almost three times the previous annual average. The catches continued at more than double the old limit for six fishing seasons. The seventh season, 1946–47, only 160,000 pounds were caught. This sudden decrease was not due to any change in effort; the year of the collapse saw the third highest number of men fishing. These men continued to fish with the same units of gear as in previous years. Actually more effort was expended in this season than in previous ones as the lake was left open in the hope that fishing would improve. Finally the local inspector decided the stock had been seriously depleted and ordered the fishing to cease.

The year following the collapse no fishing was permitted; the next year a catch of 55,000 pounds was authorized but the fish were too small to stand shipping. Accordingly, the lake was closed again for a year. It was reopened in 1950–51 and has continued each year to date. Catches quickly returned to pre-war levels and higher.

EFFECT OF EXPLOITATION ON AGE COMPOSITION AND GROWTH

The age compositions of the samples of whitefish taken from Pigeon Lake since 1942 are shown in Table III.

A study of Table III reveals two very consistent trends: (1) from 1942 to 1947 the percentage of young fish in the samples increased and the percentage of older fish decreased. Thus, in 1947, 74.5% of the sample was of two-year-olds and no fish older than six were taken. (2) From 1948 to 1954 the samples contained fewer young and more old fish. The period of decreasing age corresponds

TABLE III.—The age composition of the samples of whitefish removed from Pigeon Lake from 1942 to 1954.

Date	No. of fish	Av. age	Percentage having age[a] I	II	III	IV	V	VI	VII	VIII
Aug. 1942	100	5.1	0	8.0	2.0	17.0	28.0	37.0	8.0	0
Dec. '43–Feb. '44	330	4.4	0	0	27.3	25.5	30.3	13.2	3.7	0
Aug. 1944	127	5.1	0.8	0	1.6	33.0	26.0	26.8	11.0	0.8
Sept. 1945	102	4.3	1.0	0	11.8	52.9	23.5	8.8	2.0	0
Dec. '46–Jan. '47	301	3.9	0	13.3	21.6	40.2	13.6	7.6	3.7	0
Oct. 1947	215	2.3	0	74.5	20.9	3.3	0.4	0.4	0	0
Oct. 1948	92	2.4	3.3	57.5	32.6	4.3	2.3	0	0	0
Oct. 1949	100	4.0	0	0	26.0	49.0	23.0	1.0	0	0
Sept. 1950	127	3.8	0	0.7	35.0	54.0	9.5	0.7	1.5	0
Oct. 1951	199	4.9	0	0	2.0	21.5	59.5	15.5	0.5	0
Oct. 1952	99	4.8	0	0	4.0	21.2	56.6	15.2	2.0	0
Dec. 1953	100	5.7	0	0	0	5.0	35.0	47.0	13.0	0
Sept.–Oct. 1954	246	4.9	0	0	0.8	30.9	52.4	13.4	2.5	0

[a]There was one nine-year-old in 1949 and two in 1951.

to the years of high catches and the period of increasing age to the years of no catches or light fishing. On the basis of this evidence alone, it would be easy to conclude that the collapse of the fishery was caused by overfishing.

In Table IV the average lengths and weights at capture of each age are presented. In earlier studies of these data the scales were measured and the lengths of the fish at the end of each year of life were computed. As all the samples were taken in fall or winter, the year's growth is finished and the samples are comparable, from year to year, without corrections for partial year's growth. The calculated lengths offered no advantage and increased the amount of tabular data so they are not used in the present paper.

The data in Table IV clearly illustrate the changes in growth rate usually associated with changes in exploitation. Thus from 1942 to 1945 or 1946 there is a rapid increase in rate of growth. In 1946 a three-year-old whitefish was as big, or bigger than a six-year-old in 1942. The heavy exploitation seemed to promote a

TABLE IV.—Average fork lengths (L, inches) and weights (W, pounds) of whitefish of each age from 1942 to 1954.

Year	Age (completed annuli) II		III		IV		V		VI		VII	
	L	W	L	W	L	W	L	W	L	W	L	W
1942	11.1	—	13.7	—	14.4	—	15.5	—	16.3	—	17.0	–
1943	—	—	14.6	1.5	15.9	2.8	16.8	3.1	17.4	3.4	18.1	3.9
1944	—	—	14.5	1.9	15.9	2.4	17.0	3.0	17.4	3.3	18.3	3.6
1945	—	—	16.4	2.1	17.9	2.5	18.6	3.2	19.6	3.6	20.4	3.6
1946	15.1	1.8	16.5	2.2	17.3	2.6	18.3	3.0	19.3	3.6	20.4	3.6
1947	14.2	1.6	15.2	2.0	16.7	2.7	—	—	—	—	—	—
1948	12.9	1.1	15.0	1.9	—	—	—	—	—	—	—	—
1949	—	—	14.3	1.2	15.3	1.8	16.6	2.1	—	—	—	—
1950	—	—	14.4	1.5	14.8	1.6	15.9	2.0	—	—	—	—
1951	—	—	13.5	1.4	14.8	1.7	15.5	2.0	16.5	2.4	18.4	3.2
1952	—	—	14.5	1.6	14.9	1.8	15.4	2.0	16.2	2.4	17.1	2.9
1953	—	—	—	—	15.5	1.5	15.9	1.7	16.5	1.9	17.2	2.2
1954	—	—	14.3	1.5	14.5	1.6	15.2	1.9	16.1	2.3	16.8	2.5

much faster rate of growth, so that the fish grew in three years as much as they had previously grown in six. From 1947 to 1950 there was either no fishing (2 years) or very light catches. The growth rate slowed down again to the 1942 level and has remained there, more or less closely, for the past five years.

The general impression of decreasing age and increasing growth during heavy exploitation, followed by the reverse during light exploitation, suggests very forcibly that the collapse of the fishery in the 1946–47 season was due to overfishing. Such was the interpretation given some of these data by the author in a previous paper (Miller, 1949). However, a study of recruitment during the period of high exploitation reveals that this interpretation is not entirely true.

EFFECT OF EXPLOITATION ON RECRUITMENT

If the collapse of the fishery was due to overfishing, i.e., to reduction of brood stock, then it should be possible to demonstrate a relation between the number of spawners and the number of progeny that were subsequently taken by the fishery. The years when the fishery yielded very low catches should be those years when the progeny of the most heavily exploited brood stock would be expected to make up the catch. As a first step in exploring this possibility the total contribution to the fishery, in numbers of fish, of each of the year-classes has been calculated. The calculations were performed as follows: First all of the fish in each sample were assigned to their proper year-classes. For example, the October, 1948, sample consisted of whitefish aged I to V, and, therefore belonging to the year-classes 1947 to 1943 inclusive. Next, the average weight of the individual fish of each year-class in each sample was calculated; then, knowing the percentage of each year-class in a sample, the percentage by weight could be determined. Finally, the total weight of each year-class in the commercial catch was calculated by multiplying the figure for the total catch by the percentage of the year-class in the sample. These weights were easily converted to numbers of fish by dividing by the average weight of each year-class. An example for the year 1948–49 is shown in Table V.

TABLE V.—The contribution of the year-classes 1943–1947, inclusive, to the catch of 1948–49.

Age	Year-class	Percentage by number	Av. wt. (*lb.*)	Percentage by weight	Total weight[a]	Total numbers
I	1947	3.3	0.5	1.2	700	1,400
II	1946	57.5	1.1	44.0	28,100	25,500
III	1945	32.6	1.9	43.2	27,600	14,500
IV	1944	4.3	2.4	7.2	4,600	1,900
V	1943	2.3	2.8	4.5	2,900	1,000

[a]Commercial catch for 1948–49 was 63,800 pounds; calculations were made by slide-rule.

The calculations shown in Table V were repeated for each year of the study. It was then possible to tabulate and add together the contributions of each year-class and so arrive at the total contribution of each year-class to the fishery. The data permit such calculations for the year-classes 1936–1949, inclusive, which appeared in the fishery from 1940–1954. The contributions are shown in Table VI.

The year-class contributions in Table VI are assumed to give a measure of year-class strengths. Of course, not all the members of a year-class are caught; an unknown percentage die from other causes. However, it seems reasonable to assume that the loss caused by this unknown mortality is about the same for each year-class, in which case Table VI does give a fair measure of *relative* year-class strengths. There is one weakness in this assumption when applied to these data: during the fishing seasons 1947–48 to 1950–51, inclusive, there were two seasons of no catch and two of light catch. The year-classes 1942–1946, inclusive, are thus theoretically subjected to greater losses through natural causes, and may appear relatively weaker than they actually were. It is believed this possible discrepancy is not serious. Thus the year-class of 1946 passed through these four seasons as I to IV-years-olds, yet yielded 134,700 fish; the year-class of 1945, with almost the same history yielded only about one-quarter as many fish.

TABLE VI.—Numbers of fish contributed to the fishery by each of the year-classes 1936–1949.

Year-class	No. of years in fishery	Contribution	Remarks
1936	5+	115,600	Years 1, 2 and 3 missing
1937	5+	95,200	Years 1 and 2 missing
1938	6	133,700	Year 1 missing
1939	6	108,400	Complete
1940	5	139,900	"
1941	3	77,800	"
1942	7	40,900	"
1943	7	18,100	"
1944	7	11,140	"
1945	5	35,200	"
1946	6	134,700	"
1947	7·	156,500	Years 8 and over missing
1948	5+	88,500+	Years 7 " " "
1949	3+	104,100+	Years 6 " " "

It seems safe to conclude that the four year-classes 1942–45 were very substantially smaller than all the others. These are the year-classes which formed the bulk of the fishery during the years 1946–1950; their scarcity resulted in the collapse of the fishery. The next step is to determine if the scarcity of these year-classes was or was not due to depletion of brood stock.

A measure of the size of the broodstock can be obtained from: (a) the age composition of the catches of the commercial fishery, (b) the age at which each year-class reached maturity and spawned, and (c) the sex ratio of the spawning fish.

Let us deal first with the matter of sex ratio. In general whitefish have a 50:50 sex ratio. This has been found by Van Oosten and Deason (1939) in Lake Champlain, by Van Oosten (1939) in Lake Huron, by Van Oosten and Hile (1949) in Lake Erie, and by Kennedy (1953) in Great Slave Lake. However, if samples are taken in the fall of the year, from spawning or immediately prespawning fish, a very high proportion of males has been found in Lakes Erie and Huron (*opera citata*). The Pigeon Lake samples taken in September and October likewise show a high proportion of males; it is generally agreed that this

situation is a result of movements or groupings associated with spawning and does not give a true picture of sex ratio. Sex data are available for five samples of Pigeon Lake whitefish collected when spawning was not in progress. These are shown in Table VII.

TABLE VII.—Percentage of males of each age in five samples of Pigeon Lake whitefish.

Date	No. of fish	Percentage of males having age						Total percentage of males
		II	III	IV	V	VI	VII	
Aug. 1944	127	—	—	38.0	15.6	22.8	43.0	28.3
Dec. 1946	100	75.0	50.0	41.0	33.0	33.0	20.0	43.0
Jan. 1947	201	47.0	36.0	43.0	17.0	15.0	—	36.0
March 1948	67	64.0	58.0	22.0	20.0	25.0	—	42.0
March 1949	100	—	46.0	55.0	50.0	—	—	47.0

The data in Table VII reveal a preponderance of females which is at variance with findings in other lakes. They also show a tendency for males to decrease with increasing age. Such a tendency was also observed by Van Oosten and Hile in spawning fish in Lake Erie (*op. cit.*). The excess of females during the period of heavy fishing in Pigeon Lake may be a response to the depletion of the older age groups and, if so, it would offer an interesting explanation of the sometimes inverse relationship between brood stock strength and strength of filial generations. However, the present data are considered inadequate for firm conclusions and, in the calculations that follow, brood stock strength is based on total numbers of mature fish of both sexes. This should give safe and conservative estimates.

Of the year-classes involved in this study, 1936–1940, inclusive, were filial generations of year-classes of 1934 and earlier, for which there are no data. The earliest year-class for which data on its parent year-classes are available is 1941; the year-class of 1935, which spawned for the first time in 1940, gave rise to part of the year-class of 1941 (eggs deposited in the fall of 1940, hatched in the spring of 1941). Computation from the commercial catch data (as in Table V) shows that 43,500 of this parent year-class (1935) were caught during the winter of 1940–41; thus the parent strength of the year-class was at least 43,500 fish. Reckoning in this way it is possible to reach a minimum estimate of the parent strength for each of the filial year-classes 1941 to 1949. In these calculations it is necessary to include the effect of exploitation on age of maturity; in 1940 the fish spawned for the first time at age five; by 1943 all four-year-olds were mature; by 1945 all three-year-olds were mature; and by 1947 all two-year-olds were mature.

As a further illustration of the method of computation, consider the year-class of 1945. The catch data show that in 1944, when this year-class was spawned, the fishery took (after spawning season) 1,200 eight-year-olds, 15,500 seven-year-olds, 37,800 six-year-olds, 36,700 five-year-olds and 46,300 four-year-olds, all of which had spawned. The minimum parent stock of the year-class of 1945 is, therefore, 137,500 fish. It should be realized, of course, that such an estimate is in error from two sources; first, some of the fish that spawn escape the fishery; and, second, natural mortality between spawning time and the start of fishing would reduce the number available to the fishery. The estimates are,

therefore, too low; but the calculations of year-class contributions, shown in Table VI, are subject to the same error, so that minimum parent strength and minimum year-class yield should be relatively comparable.

The computations of brood stock numbers are summarized in Table VIII.

TABLE VIII.—Minimum estimates of the numbers of spawning fish (parent strength) that produced each of the year-classes 1941–1949.

Year-class	Number of parent fish	Remarks
1941	43,500+	1 parental year-class only
1942	77,000+	2 " " " "
1943	82,600	Assumed complete
1944	132,600	Complete
1945	137,500	"
1946	126,700	"
1947	53,800	"
1948	17,400	Estimate[a]
1949	42,900	Complete

[a]No commercial catch in 1947–48.

By combining the relevant portions of Tables VI and VIII it is now possible to compare size of parent stocks with subsequent yields of progeny to the fishery. This is shown in Table IX.

TABLE IX.—Parent strength and total yield of each of the year-classes 1941–1949 (in numbers of fish).

Year-class	Parent strength	Total yield
1941	43,500+	77,800
1942	77,000+	40,900
1943	82,600	18,100
1944	132,600	11,140
1945	137,500	35,200
1946	126,700	134,700
1947	53,800	156,500
1948	17,400	88,500+
1949	42,900	104,100+

The data in Table IX are rather remarkable in that they demonstrate no discernible relationship between brood stock and filial generations. Thus the year-class with the most parents (1945) was the third smallest recorded; the year-class with the second most parents (1944) was the smallest; conversely, the year-class with the third most parents (1946) was the second largest; and the largest year-class (1947) had a smaller than average parent strength.

The data in Table IX do not support the theory that overfishing (i.e., reduction of brood stock) caused the collapse of the Pigeon Lake fishery. The four weak year-classes, which caused the collapse, were produced by parents unaffected by the heavy exploitation and, consequently, present in normal abundance. Exploitation reduced the parent stocks of the year-classes of 1947 and 1948, but the yields of these year-classes were normal or better.

EXPLANATION OF THE COLLAPSE OF THE FISHERY

The data of Table IX are somewhat paradoxical, since it is absurd to argue that brood stock and filial generations are completely unrelated. Obviously, if brood stock is zero, then egg deposition will also be zero; conversely if brood stock is abundant, many eggs will be deposited (spawning facilities in Pigeon Lake are virtually unlimited). It follows then that the observed lack of relation between parents and progeny is due to some secondary cause. The most likely causes are widely fluctuating amounts of mortality of either eggs or fry or both; and these fluctuations are unrelated to the numbers of eggs deposited. As far as is known, in Alberta lakes, conditions during spring and summer do not fluctuate in a way which is likely to destroy fry. The only exception is prolonged ice cover in the spring, which has been observed to kill fry in some lakes. So far as is known, this has not been true in Pigeon Lake. It is assumed, therefore, that the mortality affects the eggs.

It has been shown elsewhere (Miller, 1952) that several Alberta whitefish lakes contained weak year-classes for 1942, 1943 and 1944. This widespread coincidence was shown to be possibly related to high winds in September, October and November—the months of whitefish spawning. It is postulated that the eggs are in shallow water, on firm bottom, where violent wind action would scour and destroy them. Large scale destruction of eggs by wind has been observed in Calling Lake (whitefish) and Square Lake (ciscoes).

The weak year-classes in Lakes Wabamum, Ste. Anne, Lesser Slave and Buck did not result in the collapse of the fisheries. The reason is quite simple: in these lakes the rate of exploitation was sufficiently low so that at least four, and usually five, year-classes contributed to the fishery each year. The weak year-classes thus proceeded through the fishery more or less 'sandwiched' between strong year-classes; however, noticeable decreases in yield occurred, particularly in Lake Wabamum.

In one sense, then, the collapse of the Pigeon Lake fishery was due to overfishing; when exploitation is so severe that two year-classes make up almost the whole fishery, a year-class failure leads to a failure or a sharp decline in the fishery. In Lesser Slave Lake, for example, high exploitation has reduced the tullibee fishery to a single year-class (two-year-olds); one year-class failure would eliminate the fishery. Before heavy fishing began this fishery took tullibee from three to eight years old, and a single year-class failure would have passed unnoticed.

Fluctuations in year-class strengths of whitefish have been noted particularly in Lake Erie, by Van Oosten (1948) and Van Oosten and Hile (1949). The latter authors attempted to correlate the weakest and the strongest year-classes with meteorological–limnological conditions. They were unable to demonstrate a clear-cut correlation and concluded (p. 200) "that the factors which determine the strength of year-classes are so numerous and have such complex interrelationships that it is not possible on the basis of present information to detect and evaluate the effect of any single one of them."

The year-class strengths of whitefish of Lake Winnipeg were studied by Kennedy (1954), who made estimates of year-class strength by summation of age-group data in successive annual samples in somewhat the same manner as employed in the present study. In his Fig. 6 he shows strong year-classes from 1932–39, followed by weak year-classes from 1940–1944, and then a strong year-class in 1945. This sequence is remarkably similar to the sequence described by Miller (1952) in six Alberta lakes. However, Kennedy offers an alternative explanation for the year-class frequencies that he observed: he reasons that the vagaries of sampling can account for the apparent fluctuations in strength; and that the fluctuations in catch may be due to variations in the catchability of the fish. After a careful reading of Kennedy's paper and a reappraisal of his own data, the author is convinced that the year-class fluctuations reported by Kennedy are real; and that the weak year-classes of the early 1940's in Lake Winnipeg and six Alberta lakes are part of some prairie-wide phenomenon, possibly associated with meteorological conditions.

CONCLUSIONS

1. A heavy rate of exploitation of the whitefish in Pigeon Lake caused the average age of the fish to decrease from 5.1 to 2.3 years. At the same time the fish began growing much faster and maturing at younger and younger ages (from maturity at age five to maturity at age two).
2. The seventh year of the increased exploitation yielded a very small catch; the fishery had failed. The cause of the failure was a series of several very weak year-classes in succession.
3. The weak year-classes were due to natural phenomena and were in no way caused by the heavy fishing. Parent stocks which produced these year-classes were at normal levels of abundance.
4. Heavy fishing contributes to the likelihood of collapse by reducing the number of year-classes that make up each year's catch. When exploitation is light enough so that four or more year-classes contribute to each year's harvest, then the failure of a single year-class has little effect on the fishery.
5. The number of years that a year-class appears in the catch does not seem to bear any relation to its abundance. Strong year-classes were removed in Pigeon Lake in from three to seven years; the very weak year-class of 1944 appeared in the fishery for seven years.
6. With cessation of heavy exploitation the whitefish of Pigeon Lake quickly returned to growth rates and age compositions characteristic of the pre-heavy fishing period.

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